Influence of Climatic and Non-Climatic Factors on Range Dynamics and Conservation Priorities of Long-Distance Migratory Birds

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A thesis submitted in conformity with the requirements
for the degree of Doctor of Philosophy

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2014

Abstract

Understanding factors influencing species' distributions and their dynamics over space and time is a fundamental question in ecology that is receiving renewed interest given increasing threats of global climate change to species persistence. Species are shifting their distributions in response to climate change; however in spite of general directional trends northwards and up in elevation there is substantial interspecific variation. The complexity of species' responses is challenging to explain and limits our predictive capacity to anticipate future consequences of climate change. In addition to climatic factors, species' range dynamics are influenced by non-climatic factors including the biotic interactions, demography, dispersal, and the temporal and spatial scale of threatening processes. The objective of this thesis is to test the role of climatic and non-climatic factors on seasonal range dynamics of long-distance migratory birds over multiple spatial scales, in the recent past, present, and in the future. An understanding of the determinants of Nearctic-Neotropical migratory bird distributions across their interconnected seasonal ranges remains unclear, and few climate change vulnerability assessments consider the complement of habitat dependencies required across their annual cycle.

To address these research gaps, I applied multiple modeling methods with outcomes that are increasingly process-oriented. These include correlative species distribution models, dynamic occupancy modeling that account for detection probabilities, and coupled species distribution-metapopulation demographic models. Such modeling approaches allow for deeper inferences

regarding the biological processes that actually drive shifts in species distributions over space and time.

The main findings of my thesis include: (1) biotic vegetation factors improve species distribution model predictive accuracy measures across both seasonal ranges, and this has non-negligible consequences for spatial conservation priorities under climate change, (2) determinants of seasonal distributions of migratory birds tend to be dominated by abiotic factors, while seasonal differences within species suggest a role for dynamic seasonal niches, (3) short-term habitat changes can more strongly influence local extinction probabilities relative to inter-annual variation in weather suggesting that the temporal scale of climate change and habitat loss requires careful consideration, and (4) accounting for multiple sources of uncertainties is essential for improving models and can help inform robust management actions.

Acknowledgments

There are numerous people who I have met throughout my time as a doctoral student who have imprinted themselves on me. My words are not eloquent enough to express how grateful I am to have met Yessica Rico, who has become both friend and collaborator. I am indebted to the members of the Fortin Spatial Ecology Lab for providing a supportive and stimulating environment. This includes Kate Kirby, Alexandre Martensen, Lanna Jin, Aaron Hall, Sandy Watts, Josie Hughes, Colin Daniels, Jonathan Ruppert, Amanda Xuereb, and Hawthorne Beyer. I am excited to continue our collaborations and our friendship – it is particularly brilliant when the two collide.

I have met many inspiring and hard-working friends as executive board member of the Toronto Chapter of the Society for Conservation Biology. Thank you to the following for helping provide me with meaningful distractions from thesis writing – Michelle Dileo, Ekaterina Hult, and Amanda Xuereb. I have learned much from working with you over the course of the years and truly hope that our paths keep on crossing.

And finally, to the myriad of others in my life who have been there along this journey –I owe you much and could not have done this without you. This mix of old and new school includes: Moira Coffey, Gaby Etcheverry, Corina Crawley, Karen Wigg, Robyn Mitz, Brenda Robbins, Lacy Lewis, Maurice Lewis, Isabel Black, and the Christie cats.

Chapter Acknowledgments

This thesis contains four co-authored manuscripts that are published, in review, or in preparation for submission to peer-review journals. Design, analysis, and writing were conducted by the principal author and PhD candidate. Co-authors were involved with conceptual discussions, the compilation of data sets, and participation in the review and editing of all written manuscripts. Permission to publish these manuscripts has been obtained from the publishers.

1. **Naujokaitis-Lewis, I.** and M.-J. Fortin. Multi-dimensionality of seasonal range shifts of long-distance migratory birds under climate change. *In preparation for* Global Change Biology.

2. **Naujokaitis-Lewis, I.** and M.-J. Fortin. Temporal variation of biotic factors underpins contemporary species' range dynamics. *In preparation for* Global Change Biology.

3. **Naujokaitis-Lewis, I.**, J.M.R. Curtis, L. Tischendorf, D. Badzinski, K. Lindsay, M.-J. Fortin. Uncertainties in coupled species distribution–metapopulation dynamics models for risk assessments under climate change. Diversity and Distributions 19: 541–554. Special issue: Risk assessment for conservation.

4. **Naujokaitis-Lewis, I.**, T. Martin, H. Possingham, M.-J. Fortin. Conservation planning under climate change for migratory species. *In preparation for* Nature Climate Change.

Publications related to work conducted at the University of Toronto during my PhD include:

1. Guisan, A., J. Baumgartner, R. Tingley, **I. Naujokaitis-Lewis**, et al. 2013. Predicting species distributions for conservation decisions. Ecology Letters 16: 1424–1435.

2. **Naujokaitis-Lewis, I.**, Y. Rico, J. Lovell, M.-J. Fortin, M.A. Murphy. 2012. Implications of incomplete networks on estimation of landscape genetic connectivity. Conservation Genetics 14: 287-298.

3. Anstett, D., **I. Naujokaitis-Lewis,** M. Johnson, M. 2014. Latitudinal gradients in herbivory on Oenothera biennis vary according to herbivore guild and specialization. Ecology (in press).

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Chapter 1
Introduction

1.1   The rise of global threats to biodiversity

Understanding the determinants and causal factors responsible for species distributions and their limits has a long history in ecology (MacArthur, 1972, Gaston, 2003). Renewed interest in this fundamental question is driven in large part by the pervasive reach of the human footprint, in particular the accelerating rates of global environmental impacts of climate change and habitat loss, two major drivers of biodiversity loss (Sala *et al.*, 2000, Brook *et al.*, 2008). Over the past century temperatures have increased by approximately 1°C and projections suggest large changes in mean temperature and extreme climatic events by the end of 2100 (IPCC, 2012). In addition to climate change, habitat loss is considered the current largest threat to biodiversity (Pimm & Raven, 2000, Warren *et al.*, 2001), and there is increasing concern regarding the synergistic effects of these threatening processes (Jetz *et al.*, 2007, Brook *et al.*, 2008, Mantyka-Pringle *et al.*, 2012). The broad reach of these global threats underscores the need for better understanding of species' responses to these changes and the concurrent development of stronger predictive science to anticipate consequences to inform priorities for biodiversity conservation.

1.2   Climate, climate change, and range dynamics

Understanding factors influencing species' distributions and their dynamics over space and time remains a challenging endeavor due to the multiplicity of interacting factors, and the complexity of species' responses. This information is essential for biodiversity conservation measures. Abiotic factors, in particular aspects of temperature, have long been regarded as dominant determinants of species' distributions, in particular at broad spatial scales (Andrewarth & Birch, 1954, Pearson & Dawson, 2003). Reinforcing this idea, the most commonly documented ecological responses to recent climate change include shifting distributions and phenologies (Walther *et al.*, 2002, Parmesan & Yohe,

2003). Focusing on species' distributional responses, globally, species' ranges are shifting towards higher latitudes and elevation in response to elevated temperatures (Parmesan, 2006, Chen *et al.*, 2011a). Yet despite this undeniable fingerprint of climate change, evidence is accumulating that there is substantial inter- and intra-specific variation in species' distributions (Chen *et al.*, 2011c, Mair *et al.*, 2012). For example, many species are not tracking the pace of climate change (Loarie *et al.*, 2009, Devictor *et al.*, 2012). In other cases, broad-scale responses to climate change appear idiosyncratic across species with range changes of varying magnitude and even directionality (VanDerWal *et al.*, 2013, Grenouillet & Comte, 2014). Despite the appeal of focusing on species' responses to temperature change, the variation in observed recent range changes suggests a need to move beyond an exclusive focus on the role of climatic factors on species' range dynamics (Gaston, 2003).

1.3   Non-climatic factors and range dynamics

Variation in distributional responses to climate change is likely mediated by additional factors, in part a function of the degree to which climate limits species' distributions. Biotic interactions and biotic habitat associations are increasingly recognized as influencing species distributional responses at broad scales (Araújo & Luoto, 2007, Gotelli *et al.*, 2010, Wisz *et al.*, 2013, Kissling & Schleuning, 2014). Species with strong biotic habitat associations, such as certain higher trophic level consumers (e.g., birds), may be more limited by habitat features, such as structure and composition of vegetation, even at range-wide scales (Kissling *et al.*, 2010). Consequently, in cases where species are reliant on biotic habitat features and where habitat is limiting, we might expect to see incomplete tracking of suitable climate, resulting in disequilibrium in relation to suitable climate (Warren *et al.*, 2001, Guisan & Thuiller, 2005). Such a situation may be amplified when we consider the spatial heterogeneity in patterns of habitat loss and fragmentation, which have the potential to counteract positive population responses at favourable leading (i.e. warm) edges resulting in diminished expansion potential (Thomas *et al.*, 2001, Hampe & Petit, 2005, Melles *et al.*, 2011). Biotic habitat dependencies may further result in amplified mismatches between species distributions and suitable climate

given the longer expected lags in plant species' responses to climate change (Boulangeat *et al.*, 2014). Biotic interactions, such as predation and competition, may constrain species' distributions and both within- and between-trophic level interactions are expected to be modified in complex ways due to climate change (Gilman *et al.*, 2010). When interacting species respond in divergent ways to climate change, the nature of their interaction may be modified. For example, spatial mismatches may occur due to different distributional responses of obligate species (Schweiger *et al.*, 2012, Wisz *et al.*, 2013). Furthermore, the inclusion of biotic habitat elements refines species distribution model outcomes to more closely reflect the area of occupancy by capturing proximate resource dependencies (Heikkinen *et al.*, 2007, Luoto *et al.*, 2007, Barbet-Massin *et al.*, 2012b) and is considered the dominant driver in population-level abundances and demographic changes relative to climate (Eglington & Pearce-Higgins, 2012, Mair *et al.*, 2014). Despite the predominant use of abiotic factors to describe species distributions at broad scales (e.g., Elith & Leathwick, 2009, Austin & Van Niel, 2011), it is increasingly argued that to develop informed capacity to predict species responses to climate change requires incorporation of biotic factors (Gilman *et al.*, 2010, Wisz *et al.*, 2013).

To date, the majority of studies addressing broad-scale species' responses to climate change have focused on long-term average climate conditions, typically focusing on a univariate dimension of climate (i.e. mean temperature) (Parmesan *et al.*, 1999, Thomas & Lennon, 1999, La Sorte & Thompson, 2007, Chen *et al.*, 2011b). Increasing evidence for the high dimensionality of range-shift patterns and variation in directional shifts suggests that understanding range dynamics using these variables offers a limited perspective and potential for inference (VanDerWal *et al.*, 2013). From an ecological perspective, short-term weather and long-term climate have long been recognized as important limiting factors to species distributions (Birch, 1957, Stenseth *et al.*, 2002). In addition to the significance of long-term trends on species distributions, finer temporal scale such as sub-annual and inter-annual variability are likely important for many species (Jackson *et al.*, 2009, Dobrowski, 2011). Indeed, population abundances and underlying demographic processes are influenced by short-term variation and temporally

fluctuating abiotic conditions (Anders & Post, 2006, van de Pol *et al.*, 2013). Furthermore, extreme events (Jentsch *et al.*, 2007), such as droughts and heat waves, occurring over short time frames can result in negative population-level consequences and result in local extinctions (Albright *et al.*, 2010, Doak & Morris, 2010, McKechnie *et al.*, 2012, Cunningham *et al.*, 2013). Increased temporal and spatial autocorrelation of climate change may also contribute to synchronization of population dynamics, which may contribute to increased risk of extinction (Post & Forchhammer, 2004), further highlighting the complexity of impacts of changing climate. In addition, temporal dimensions of habitat are important for species relying on disturbance dependent or successional habitats, while anthropogenic land-use change may contribute to landscape-level changes largely independent of climate (e.g., Santika *et al.*, 2014). Consequently, it is not surprising that incorporating temporal variability in habitat dynamics influences species distributions and models accounting for such dynamics improve outcomes (Vallecillo *et al.*, 2009, Price *et al.*, 2013, Porzig *et al.*, 2014). While identifying relevant temporal scales for measuring climate or habitat parameters requires insight into species' biology and traits, temporal scale and variability of extrinsic conditions is of emerging importance in understanding consequences of global changes on species' ranges.

Spatial and temporal heterogeneity of extrinsic conditions (i.e., threats to species persistence such as climate change and habitat loss) influence the pattern of species distributions and the underlying population-level processes that drive range dynamics in complex ways. Range dynamics are a consequence of spatial patterns of birth, death, and dispersal (Holt *et al.*, 2005). Range shifts are typically driven by population dynamics occurring at the range edges, where dispersal capacity and propensity is integral to colonization of new habitats (Kubisch *et al.*, 2014). Range shifts thus occur when there is spatial structuring of local rates of extinction or colonization, which may relate to patterns of land-use change resulting in loss of habitat, climate change, or gradual changes in marginal habitat. However, rates of shift at different boundaries are not uniform; multidimensional assessments of ranges along latitudinal, longitudinal, and elevational or depth dimensions are lacking presenting a limited view of ecological and

evolutionary significance of pattern and process (Hampe & Petit, 2005, Lenoir & Svenning, 2014). For example, compensatory demographic rates may buffer against negative consequences of climate warming, consequently slowing rates of range shift at the warm edge (Doak & Morris, 2010). Furthermore, climate stress or habitat loss may not be relegated to boundary populations but may occur throughout the range (Lenoir *et al.*, 2008), resulting in more complex patterns of range change (Maggini *et al.*, 2011, Grenouillet & Comte, 2014, Lenoir & Svenning, 2014). Changes in abundances across species' ranges are increasingly observed (Jiguet *et al.*, 2010, Virkkala & Rajasärkkä, 2011, Mair *et al.*, 2014). These changes may indicate initial stages of range shift (Maggini *et al.*, 2011), and underlie the importance of population-level data to refine predictions of future changes under climate change (Huntley *et al.*, 2010, Howard *et al.*, 2014). Adding to the complexity, spatial and temporal variation in extrinsic conditions may differentially influence life-history stages or vary by season, such as in the case of migratory species (Wilson *et al.*, 2011). A range wide perspective on temporal range shifts can inform on spatial variation in processes driving dynamics and is crucial to understanding species' vulnerabilities to threatening processes. Yet, studies documenting patterns of species' distributional change over space and time at the range-wide scale remain sparse (Lehikoinen *et al.*, 2013, Grenouillet & Comte, 2014). Consequently, this remains an outstanding challenge for ecologists and global change scientists with fundamental consequences for biodiversity conservation.

To gain a more synthetic understanding of observed variations in range shifts and development of stronger capacity for prediction requires broad-scale studies capturing the complete range. Scientists currently have access to unprecedented types of biodiversity data on species distributions, and increasingly, global scale data describing fine-scale environmental conditions. Predominant approaches to understand species' contemporary response to global change have typically applied species distribution models (SDMs) that correlate environmental conditions with species' occurrences (Guisan & Thuiller, 2005, Elith & Leathwick, 2009). While valuable, these approaches are generally applied in static ways without consideration of temporal dynamics of extrinsic factors, population

processes, or dispersal (Franklin, 2010). As range shifts result from a complex interplay between biological and environmental constraints, the use of data reflecting these dynamics is desirable. While there is a clear need for integration of demographic data for prediction (Huntley *et al.*, 2010, Pagel & Schurr, 2012, Schurr *et al.*, 2012, Fordham *et al.*, 2013), there is a general paucity of such information.

1.4   Thesis outline

The objective of this thesis is to gain a better understanding of the role of climatic and non-climatic factors on long-distance migratory bird range dynamics, in the recent past, present, and in the future. In addition to the ecological advances related to the field of species' range dynamics, an underlying theme of this thesis is the importance of different sources of uncertainty on the robustness of our inferences and predictive outcomes. The use of increasingly process-oriented, mechanistic modelling approaches will allow an exploration of the trade-offs between model complexity, generality, tractability, and predictive accuracy. Such modeling approaches allow deeper inferences regarding the biological processes that actually drive shifts in species distributions over space and time. This research contributes to the body of literature that is advancing our ecological understanding of species' responses to global changes, methodological developments that address multiple forms of uncertainty that may impact our predictive capacity, and perhaps more importantly, the implications of these outcomes to management decisions and actions aimed at minimizing extinction risks.

In this thesis, I focus on long-distance migratory birds as model organisms, specifically species from the *Parulidae* family, or wood-warblers (see Chapter 2 Table 2.1). Birds possess a number of advantages that makes them amenable to analyses of range dynamics. Although they are a relatively well studied taxonomic group (Faaborg *et al.*, 2010b), an understanding of the determinants of Nearctic-Neotropical migratory bird distributions across their multiple seasonal ranges remains unclear (Faaborg *et al.*, 2010a). Furthermore, there are few studies that apply a complete life cycle approach to inform on potential sensitivities to multiple stressors of climate change and habitat loss at

range-wide scales, resulting in incomplete risk assessments (Small-Lorenz *et al.*, 2013a). Long-distance migratory birds may be especially vulnerable to climate change relative to resident or short-distance migrant species (Lemoine & Böhning-Gaese, 2003, Visser *et al.*, 2009). It has been suggested that their reliance on spatially disjunct wintering ranges located far from breeding sites may increase their vulnerability to future climate changes related to an inability to predict changes in timing of food resources in breeding regions (Albright *et al.*, 2010, Visser *et al.*, 2010). Recent evidence suggests that the timing of spring migration arrival of long-distance migrants has changed less compared to short-distance migrants (Saino *et al.*, 2011). This inability to adjust migration phenology to track advancing spring on the breeding grounds suggests lowered phenological plasticity in spring arrival times (Gwinner, 1996), and potential for population declines (Miller-Rushing *et al.*, 2008, Both *et al.*, 2010, Saino *et al.*, 2011). Additionally, they are exposed to multiple effects of climate change across each seasonal range, where carry-over effects of threatening processes occurring in one season can have population-level consequences in the other season (Wilson *et al.*, 2011). The relatively complete occurrence records collected through voluntary monitoring programs across much of their range allows testing of hypotheses examining the role of determinants of range limits and processes contributing to range shifts over multiple spatial and temporal scales.

1.5   Synthesis of chapters

Migratory birds spend different periods within an annual cycle in spatially and ecologically distinct areas, often separated by long-distances. Given the interconnectedness of population processes and limitations across these seasonal ranges (Sherry & Holmes, 1996, Sillett *et al.*, 2000, Norris *et al.*, 2004), such as carry-over effects from the wintering grounds on reproductive success (Marra *et al.*, 1998, Norris *et al.*, 2004), comprehensive assessments of threats to species persistence are required across their complex habitat dependencies within the annual cycle (Small-Lorenz *et al.*, 2013a). Despite this, the influence of potential future climate changes predictions are typically based on a single season thereby providing only a partial view of possible vulnerabilities (e.g., Venier *et al.*, 1999, Austin & Rehfisch, 2005, La Sorte & Thompson,

2007, Zuckerberg *et al.*, 2011) but see Doswald *et al.* (2009). The objectives of Chapter 2 are two-fold: (1) to assess the relative importance of abiotic and biotic vegetation factors on contemporary species' distributions across the breeding and non-breeding ranges of 33 species of *Parulidae* and (2) to partition the influence of multiple sources of uncertainty on predicted outcomes. Contributions of this chapter include advances in the fields of biogeography and global change science and emphasize the importance of including direct habitat features for secondary consumers in both understanding determinants of broad-scale species' distributions both contemporarily and under potential future climate change. I address multiple sources of uncertainty in this chapter, including modeling algorithm, choice of general circulation models, parameterization of a dispersal model, and model selection, as well as sensitivity of various metrics used to quantify range shifts.

In Chapter 3, I examine how temporally varying extrinsic factors influence range-wide extinction and colonization processes. I focus on two sister species, *Vermivora chyrsoptera* and *V. pinus*, as a model system. Specifically, *V. chrysoptera* is undergoing precipituous declines and large range shifts in contrast to *V. pinus* that is relatively stable with respect to global population size and range dynamics. I developed dynamic state-space occupancy models to test multiple competing hypotheses regarding the relative importance of major drivers of range shifts: extreme temperature, habitat, and occurrence of congeneric species for a 30-year period, 1983 to 2012. The novelty of this chapter includes addressing the complexity of range dynamics between potentially interacting species with a demographic process-oriented approach that integrates detection errors, the latter which can bias estimates of covariate influences and under-estimate species distributions (Kéry *et al.*, 2013). The outcomes of this work underscore the need to consider temporal scale of non-stationary extrinsic conditions demonstrating the strong relative importance of biotic factors relative to extreme temperature in driving contemporary range dynamics.

While broad-scale SDMs can provide general patterns and linkages with large-scale determinants of ranges such as abiotic conditions, integrating climate change

predictions with population dynamic models can provide finer-scale predictions of species persistence, and potentially more accurate predictions (Morin & Thuiller, 2009, Mustin *et al.*, 2009, Gogol-Prokurat, 2011). Such a landscape level analysis allows testing of hypotheses related to climate and habitat limitations on species persistence and range shifts, and is also reflective of the scale at which conservation and management actions are taken. Given the importance of population dynamics at the range margins for determining species' responses to climate change (Holt & Keitt, 2000, Holt *et al.*, 2005), in Chapter 4, I investigate the interaction of climate and habitat changes on the persistence of Hooded Warbler (*Setophaga citrina*) populations at its northern and expanding breeding range margin (Melles *et al.*, 2011) by developing hybrid SDMs integrated with metapopulation demographic models. Metapopulation theory suggests that variability of site-level occupancy can occur as a function of unsuitable environmental conditions and demographic consequences (Hanski, 1999). Recent work has shown that climate limitation is not occurring at the northern edge of the Hooded Warbler's range whereas habitat elements, including amount and configuration, are hypothesized constraints to further range expansion. The research questions addressed in this chapter include: (1) can occupied populations track predicted climate changes, (2) how does the interaction between scenarios of habitat availability and future climate change influence predicted range expansion, (3) how congruent are predictions of range expansion between SDM and SDM + population dynamics (hybrid) models in terms of predictive accuracy and spatial congruency of predictions of range shift, and (4) how sensitive are hybrid model outcomes to multiple sources of uncertainty, including demographic parameters, amount and configuration of habitat, choice of general circulation model. My findings confirm predictions that habitat is a main constraint on population-level range expansions relative to climate factors and underscore how demographic approaches to model range expansions reduce capacity for over-prediction under SDMs that assume equilibrium between species and suitable climate habitats. The methods developed to address uncertainty using global sensitivity analysis framework highlight the importance of demographic uncertainties on predictions of extinction risk.

Migratory bird species present a unique challenge for conservation planning under climate change due to their life histories. Many species rely on disjunct breeding and nonbreeding habitats where regional variation in future climate across temperate and equatorial expanses may result in asymmetric range shift patterns. Despite the ecological significance of accounting for seasonal habitat dependencies, few studies characterize vulnerability to projected climate exposure across the annual cycle (Small-Lorenz *et al.*, 2013a). As a result this factor is largely ignored when identifying spatial conservation priorities under climate change, limiting their potential utility. Furthermore, the range dynamics of vegetation dependent species will be constrained by a combination of climate change and habitat availability, yet biotic factors are rarely included in predictive models that are subsequently used as inputs to spatial priorities. The objectives of Chapter 5 include, (1) quantifying the sensitivity of spatial priorities under projected climate change to integration of biotic vegetation factors, (2) identifying regions of priority robust to climate change across both the breeding and nonbreeding season, and (3) evaluating the performance of the current network of protected areas under climate change.

Finally, I conclude my thesis with Chapter 6 where I synthesize my overall findings and discuss avenues for future research.

Chapter 2

2 Seasonal range shifts of long-distance migratory birds under climate change: Role of uncertainties

2.1 Abstract

Migratory species may be particularly vulnerable to the effects of climate change as they are exposed to its effects over their seasonal distributions. Evaluating species vulnerabilities to the dynamic threat of global climate changes requires threat assessments over the full complement of habitats required across the annual cycle of a given species. Outcomes of species distribution models can be applied as a component of species vulnerability assessments to climate changes; yet the pervasiveness of uncertainties can compromise their application in a conservation context. While common sources of uncertainties include model selection, model algorithm, and General Circulation Models (GCMs) have been previously considered this has not been in the context of seasonal ranges. I tested the assumption of climate as a dominant factor and compared the consistency of predictions and projections under future climate changes for sets of models consisting of climate variables, habitat variables (derived from vegetation data), or climate and habitat variables together. Predictive performance was highest for climate-habitat models across both seasons, however variations in relative importance of different predictors suggests that limiting factors are seasonally dependent. Regardless of seasonal range relative range size is expected to decline, with climate-only models resulting in more extreme estimates of change. While my results are broadly consistent with previous work with large amounts of variation resulting from model algorithm and GCM, the relative importance of different sources of variation varied as a function of the seasonal range considered and was dependent on the metric of range change used as the response. These results underscore the potential bias that may be incurred in projected exposure estimates associated with multiple sources of uncertainty and the need to consider a diversity of metrics that describe multiple dimensions of range dynamics.

2.2 Introduction

Evaluating species vulnerabilities to the dynamic threat of global climate changes requires threat assessments over the full complement of habitats required across the annual cycle of a given species. Seasonal migratory species (hereafter migrants) move cyclically between geographically separated habitats over different portions of their lifecycle, which may include the use of breeding and nonbreeding ranges as well as areas along their migratory routes. Long-distance migratory birds pose a particular challenge for vulnerability assessments in part because their wide-ranging behaviors result in seasonal habitat dependencies that often cross geo-political boundaries, which can impede the identification of threats to species viability (Calvert *et al.*, 2009). Although our understanding of factors limiting bird populations are largely from studies focused on the breeding season (Faaborg *et al.*, 2010a), the processes that limit and regulate long-distance migrant populations derive from events occurring on both the breeding and wintering grounds (Holmes, 2007, Robinson *et al.*, 2008). Furthermore, evidence increasingly illustrates the fitness consequences of carry-over effects from one season to another on migratory species (Norris, 2005, Bogdanova *et al.*, 2011, Legagneux *et al.*, 2011). The fundamental importance of dynamics occurring within and interacting between seasonal phases underscores the relevance of full lifecycle assessments in climate change vulnerability assessments.

Despite increasing evidence of range shifts due to recent climate change few studies consider all seasonal habitats. Studies documenting range shifts due to recent climate changes abound and include evaluations in the western hemisphere during the breeding season (Peterson, 2003, Hickling *et al.*, 2006, Hitch & Leberg, 2007, Jetz *et al.*, 2007, Devictor *et al.*, 2008) and nonbreeding season (La Sorte & Thompson, 2007, La Sorte *et al.*, 2009, Zuckerberg *et al.*, 2009, La Sorte & Jetz, 2012); as well as in Europe and Africa during the breeding season (Lemoine & Böhning-Gaese, 2003, Huntley *et al.*, 2008, Barbet-Massin *et al.*, 2012b) and nonbreeding season (Austin & Rehfisch, 2005). Despite the clear indication of the role of climate on species range shifts, few studies examine its influence on both the breeding and nonbreeding portions of the annual cycle

for the same suite of species using the same methods (but see Doswald *et al.*, 2009). Similarly, projections of potential distributions due to future climate changes have tended to focus on one season of the annual cycle including migrants in Mexico (Peterson *et al.*, 2002), North American breeding season (Lawler *et al.*, 2009), and European breeding season (Barbet-Massin *et al.*, 2012b), as well as nonbreeding season (Barbet-Massin, 2009). Given that population-limiting processes occur over the combination of seasonal habitats (Holmes, 2007), omission of climate change vulnerability assessments across seasonal habitats represents a knowledge gap biasing our understanding of potential risks (Small-Lorenz *et al.*, 2013b).

Spatial variation in environmental conditions, land-use patterns, and projections of future climate change underscore the importance of accounting for all seasonal range dependencies in vulnerability assessments for wide-ranging migrants. Climate change is expected to vary spatially across the globe, which can affect seasonal distributions of wide-ranging migrant bird species in different ways. Climate model outcomes project larger temperature increases over much of Canada relative to temperature changes in South America by the end of this century (IPCC, 2007b). While Canada is generally expected to become wetter, projections for Mexico and Central America, where the majority of Nearctic-Neotropical birds overwinter, indicate that that these regions will become drier both annually and over the months when species over-winter (IPCC, 2007b). This asymmetry, in both the direction and magnitude of change in climate factors across the seasonal ranges of migrants, can lead to mismatches in peak resource availability on breeding grounds and timing of migration from nonbreeding grounds (Strode, 2003). Such mismatches may be more pronounced for long-distance migrants where endogenous controls, such as photoperiod, as well as climate are important for migration initiation (Studds & Marra, 2011), and can negatively influence migrant abundance (Both et al., 2006) and population dynamics (Moller, 2008, Jones & Cresswell, 2010, Saino *et al.*, 2011). Furthermore, global spatial variation in future land-use conversion (Jetz et al., 2007) could lead to loss of habitats disproportionately affecting habitats required across a given seasonal range. Given the lack of uniformity in direction and magnitude of threat dynamics, assessing how vulnerability across all

habitats required over the annual cycle of migrant species is crucial for initial risk evaluations.

Outcomes of species distribution models (SDMs) can be applied as a component of species vulnerability assessments to climate changes (Thomas *et al.*, 2010, Dawson *et al.*, 2011), however, the pervasiveness of uncertainties can compromise their application in a conservation context. SDMs, which use correlative relationships between environmental factors and species occurrences (Guisan & Thuiller, 2005, Elith *et al.*, 2006, Austin, 2007) and in combination with climate models, can be used to project future distributions under different climate change scenarios. Through the exploration of the potential for change in suitable habitats in relation to changing climates, SDM outputs contribute to an understanding of climate exposure, an element of species vulnerability assessments to climate changes (McCarthy *et al.*, 2001, Williams *et al.*, 2008b). Despite the widespread use of SDMs, their utility can be compromised by the propagation of uncertainty related to type of occurrence data used (presence-only vs. presence-absence), variable selection, sampling bias, SDM methodologies including modeling algorithms, and model parameterizations (Guisan *et al.*, 2007, Synes & Osborne, 2011, Braunisch *et al.*, 2013). In addition, General Circulation Models (GCMs) further contribute to the variability in outcomes (Beaumont *et al.*, 2008). Given the myriad sources of uncertainty, it becomes imperative to understand the types of uncertainties that influence predictions. Additionally, there are an assortment of metrics to quantify facets of range shifts, such as relative range size change, distance and direction of centroid shift, range margin shifts, and species turnover (e.g, Diniz-Filho *et al.*, 2009, Potter & Hargrove, 2013, Watts *et al.*, 2013). These metrics are frequently applied to quantify range changes, and thus provide information on individual species vulnerability or composite measures of community shifts. As these metrics measure different aspects range changes (e.g. range size vs extreme boundary shifts), there is the potential for variation in their sensitivity. A systematic assessment of common sources of uncertainty of model inputs and outputs is essential for identifying the principal sources of uncertainty and can provide insights into vulnerability characterizations.

Species distributions are the result of a complex set of factors relating both to the biology of the species and its relationship with external environmental conditions. that interact over spatial scales (Gaston, 2003). The classic perspective on factors that determine species' distributions conforms to the idea that at broad spatial scales, species distributions are predominantly structured by abiotic factors, with biotic vegetation factors and biotic interactions increasingly important at smaller scales (Grinnell, 1914, Pearson & Dawson, 2003). Despite this assertion, evidence is accumulating that the imprint of biotic factors is perceptible even at broad spatial scales and extents (Wisz *et al.*, 2013). Although climate factors exert a dominant influence on species distributions at broad spatial scales (Araújo *et al.*, 2009, Pigot *et al.*, 2010, Jiménez-Valverde *et al.*, 2011), model predictive accuracy tends to increase when climate and land-cover variables are included, in particular at finer-scale resolutions (Thuiller *et al.*, 2004, Venier *et al.*, 2004, Heikkinen *et al.*, 2007, Luoto *et al.*, 2007, Preston *et al.*, 2008, de Araújo *et al.*, 2014). The decision to include certain predictors over others is non-trivial and remains an under-appreciated source of uncertainty (but see Braunisch *et al.*, 2013), in particular with respect to the role of biotic factors, which still often remain overlooked or marginalized (Brown *et al.*, 2011). Furthermore, variation in predicted future range shifts or estimates of suitable habitat when models only include abiotic variables versus those that incorporate a combination of abiotic-biotic factors (e.g., Preston *et al.*, 2008, Barbet-Massin *et al.*, 2012b) underscores the importance of addressing this source of variability for species vulnerability assessments. Such variation may be of particular importance for species occupying seasonal habitats spanning large distances; integrating habitat variables can help to improve our understanding of factors influencing current distributions and predictions under global changes.

Here, I assess the vulnerability of 33 Nearctic-Neotropical long-distance migratory bird species (hereafter migrants) to the potential influence of future climate changes across the breeding and nonbreeding ranges separately. Nearctic-Neotropical migrant birds spend a portion of their time breeding in the northern hemisphere, migrating in the fall to the wintering grounds, and then return during spring migration to the breeding grounds. I focus on these species due to their documented declines (North

American Bird Conservation Initiative, 2009), their sensitivity to landscape features in both breeding (Flather & Sauer, 1996) and nonbreeding seasons (Robbins *et al.*, 1989), and negative impacts of recent climate changes on populations (Jones & Cresswell, 2010, Saino *et al.*, 2011). Birds are a relatively mobile group of species and recent work illustrates their ability to track recent historical climate changes (Tingley *et al.*, 2009, VanDerWal *et al.*, 2013). The capacity to track environmental conditions makes them an ideal study group to address the role of climate change on range dynamics. The overall objectives of this chapter were to expand our understanding of abiotic and biotic variables migratory species' seasonal ranges and to examine the relative importance of multiple sources of uncertainties on model projections under climate change. Specifically I ask the following questions: (1) Are there differences in the relative importance of abiotic and biotic (i.e., vegetation) variables between breeding and nonbreeding seasonal distributions ?; (2) Is climate change expected to influence seasonal distributions differently in terms of direction and magnitude of potential range shifts?; and finally, (3) How do multiple metrics of range shifts vary in relation to three main sources of uncertainty, (i) model selection contrasting abiotic models and abiotic-biotic vegetation models, (ii) choice of modeling technique, and (iii) selection of GCMs. I expected different variables to drive species seasonal distributions, resulting in asymmetry in projected range shifts under climate change. Furthermore, I expected different range shift metrics to be differently sensitive; metrics describing extreme in particular range margin boundary changes are expected to be highly variable.

2.3   Methods

2.3.1   Focal species data

I selected 33 long-distance migratory *Parulidae* species that breed in the northern hemisphere and over-winter in Central and South America (Table 2.8.1). *Parulidae* species with permanent resident populations or short-distance migrants where breeding and nonbreeding ranges were abutting one of the other were omitted to minimize the potential for confounding the seasonal association of occurrences. However, for all species I considered their complete seasonal ranges to capture the full extent of their

distributional requirements (Sánchez-Fernández *et al.*, 2011). To ensure adequate representation across the entire breeding ranges, including the northern range limits, occurrence data for the breeding season were retrieved from the North American Breeding Bird Survey data (BBS; USGS Patuxent Wildlife Research Center, 2012) and the Ontario Breeding Bird Atlas (OBBA; Bird Studies Canada *et al.*, 2008). BBS data were compiled for the years 1981-2005 and for the months of May-July, which represent the primary breeding month (Poole, 2005). The BBS is a longitudinal Citizen Science monitoring program with coverage including southern Canada and the USA since 1968. Every year, volunteers record detection data across more than 5200 predefined routes. Censuses are performed during the breeding season and most routes are re-visited annually. BBS occurrence data were compiled for the years 1981-2005 and data that conformed to the BBS standards for weather, date, time, and observer criteria were included. The OBBA is a compilation of breeding bird surveys undertaken by volunteers over the province of Ontario, where 10-km square grids are surveyed for breeding birds over a five-year period. Each grid is searched for a minimum of 20 hours over the five-year period. Two atlases have been completed to date, Atlas 1: 1981-1985 and Atlas 2: 2001-2005.

As there were no consistent surveys applied over the nonbreeding ranges, I used data collected through the eBird Citizen Science initiative (Sullivan *et al.*, 2009), which were downloaded via the Global Biodiversity Information Facility portal (GBIF; www.gbif.org). Data were screened to include only those collected between 1981 and 2005, inclusive, to ensure temporal consistency with breeding occurrence records, and environmental variables. Data from the primary wintering months, November to February, were selected as these represent the time period when most migrant birds are on their nonbreeding grounds post fall migration (Poole, 2005). To ensure a minimum level of data quality and to minimize the likelihood of capturing migrant occurrences, I only included occurrence records if they overlapped with NatureServe extent of occurrence range maps (Ridgely *et al.*, 2007).

2.3.2   Environmental data

Environmental variables were selected based on their potential to directly or indirectly affect bird distributions across the breeding and nonbreeding seasons (e.g., Root, 1988, Venier *et al.*, 2004, Huntley *et al.*, 2008, Jiménez-Valverde *et al.*, 2011, Studds & Marra, 2011). Abiotic variables included temperature seasonality, precipitation seasonality, mean of monthly maximum temperature, and mean of monthly total precipitation. Temperature seasonality was calculated as standard deviation of the monthly mean temperatures and precipitation seasonality is expressed as a coefficient of variation calculated as the standard deviation of the monthly precipitation estimates expressed as a percentage of the annual mean. Maximum temperature and total precipitation were averaged over seasonal time periods reflecting the months associated with the breeding (May-July) and non-breeding (November-February) periods of the annual cycle (Heikkinen et al., 2006). Baseline climate data for the current time period (1950-2000) were obtained from the Worldclim database, which is a set of high resolution interpolated climate data (Hijmans et al., 2005), at a spatial resolution of 10 arc-minutes. The data were subsequently averaged across all cells following Hijmans *et al.* (2005).

Projections of future climates were based on four GCMs using the A2 emission scenario for the IPPC 4th Assessment, which depicts an intensive-fossil use future with moderate economic growth (Nakicenovic *et al.*, 2000). I selected the CCMA-GCM3, CSIRO-3K, Hadley-MK3, and NIES-99 models, as they provide a range of conditions and variability with respect to annual temperature and cumulative precipitation predictions (IPCC, 2007a). Climate data from each GCM were downscaled using the delta statistical method, which is based on thin plate spline spatial interpolation of anomalies of original GCM outputs (Ramirez & Jarvis, 2008). Future projections of climate suitability were based on averages describing two thirty-year time periods defined as the 2050s and 2080s. All spatial data were downloaded at a 10-arc-minute resolution and summarized to a common resolution of 20 x 20 km cells.

Habitat data were sourced from GlobCover, a high-resolution (300 m) dataset with global coverage (European Space Agency, 2008), which provided a consistent land-cover classification method across the entire western hemisphere (Table 2.8.2). I derived biotic (i.e., vegetation) variables representing landscape composition and a measure of diversity by calculating the percent cover of forests and shrubs found within each 20 x 20 km grid cell. These cover types represent preferred broad habitat types for all focal species regardless of seasonal range. Landscape compositional heterogeneity was calculated as the number of land cover classes summarized over each grid cell. Pearson correlations amongst all pairs of predictors variables resulted in $r < |0.6|$. All spatial data were aggregated to a common resolution of 20 x 20 km and transformed to the Behrmann Equal Area projection.

2.3.3   Species distribution models

To capture variation associated with the selection of modeling algorithms, I applied five different SDMs algorithms implemented in the '*biomod2*' R package (Thuiller *et al.*, 2012): two regression methods (Generalized Linear Models, GLM (McCullagh & Nelder, 1989); and Generalized Additive Models, GAM (Hastie T, 1990)) and three machine-learning methods (Random Forests, RF (Breiman, 2001); Generalized Boosted Regression Models, GBM (Elith *et al.*, 2008); and MaxEnt (Phillips *et al.*, 2006)). I used the default settings for each modelling algorithm, except for the following changes: for Random Forests the number of trees was changed to 500, in MaxEnt only hinge and product features were specified to reduce over fitting by ensuring a smoother response curve function (Elith *et al.*, 2011). GLMs and GAMs were calibrated using a binomial distribution and logistic link function, and quadratic relationships and bivariate interactions were specified for the continuous variables. For GAM, the maximum smoothing function was set to 4 which was then optimized within the model. Finally, tree complexity of GBMs was set to two allowing up to second order polynomials and the minimum number of trees was set to 2000 following specifications in Elith *et al.* (2008).

All models were calibrated across the geographic region considered accessible and within the dispersal abilities of all focal species (VanDerWal *et al.*, 2009, Barve *et al.*, 2011, Elith *et al.*, 2011). Given the relatively high mobility of long-distance migrants, the calibration region for each species was constrained to ecoregions (Olson *et al.*, 2001) which overlapped with occurrence records (Anderson & Raza, 2010). Absence data across the breeding season included BBS routes and Atlas grid cells found within the calibration region where no occurrences were recorded for any given species over the period of analysis. To minimize sample selection bias due to lack of systematic sampling I sampled pseudo-absences across the non-breeding range of each species using the target species approach (Phillips *et al.*, 2009). Given the close phylogenetic relationships and similar ecological traits across the focal *Parulidae* species (Lovette *et al.*, 2010), and a combination of high rate of overlapping distributions in the relatively smaller ranges over the nonbreeding season, I considered all species as belonging to the target group. Maps of nonbreeding occurrences were evaluated for potential spatial errors by an expert (Dr. Jim Rising, University of Toronto, *personal communication*).

To evaluate sensitivity of model predictive outcomes and projections of range shift under climate change to variation associated with the inclusion of biotic vegetation factors, I compared models calibrated across three sets of predictor variables describing: (1) biotic factors (habitat-only), (2) abiotic factors (climate-only), or (3) both, (climate-habitat) (Table 2.6.1). To evaluate the predictive performance of each model for each species and each seasonal range, I used a five-fold cross-validated random subset of 70% of the data to calibrate the model and the remaining 30% for model testing. Each of the replicated data partitions was used to calculate mean predictive performance of the cross-validations. Models were assessed based on two discrimination capacity statistics, the true skill statistic (TSS) and area under the curve (AUC) of the receiver operating characteristic (ROC) plot on the cross-validated data (Fielding & Bell, 1997, Allouche *et al.*, 2006). AUC is a threshold independent metric and the ROC plots compare the true positive predictions against the false positive predictions across all possible thresholds. AUC varies between 0 and 1, where 0.5 represents models with predictions no better than random and 1 models that fit data perfectly. TSS corresponds to the sum of sensitivity

(proportion of presences correctly predicted, i.e. true positive rate) and specificity (proportion of absences correctly predicted, i.e. true negative rate) minus one. TSS varies between 0 (random predictions) and 1 (perfect agreement), and is considered insensitive to prevalence. Finally, the point-biserial correlation coefficient (COR) was calculated based on Pearson correlations between the presence-absence data and predicted values (Zeng & Agresti, 2000). Whereas AUC only considers predicted values, this metric provides information on both discrimination capacity and calibration as it is a function of both actual and predicted values (Elith *et al.*, 2006, Phillips & Elith, 2010). The hypothesized improvement in predictive performance with the inclusion of biotic factors to abiotic models was tested across the three variable sets using Wilcoxon's signed rank test.

Model were projected across the entire western hemisphere for the current time period, the 2050s, and the 2080s, based on the final model run using 100% of the data (Araújo *et al.*, 2005). This resulted in a total of 11880 models based on all possible combinations of factors tested, i.e., 2 seasons × 3 variable sets × 5 model algorithms × 4 GCMs × 3 time periods × 33 species.

2.3.4   Dispersal modelling

To account for processes that may limit the potential for range shifts, I modeled dispersal for each species and linked these dynamics with SDM predictions of range changes over space and time. Effectively, this reduces the predicted current and future distributions to areas that are currently occupied or may be colonized as they are within estimated dispersal distances, which represents an important step in incorporating more ecological realism (Franklin, 2010). Furthermore, this provides a transparent and non-arbitrary method for constraining predictions. I used a dispersal model based on a cellular automaton implemented in the R package '*Migclim*' (Engler *et al.*, 2012). I specified a maximum dispersal distance of 20 km/year as this generally corresponds to between-year observed and expected dispersal distances estimated for one of the focal species, Hooded Warbler (*Setophaga citrina*) (Bowman *et al.*, 2002, Melles *et al.*, 2011), and due to the resolution of the data. The dispersal estimates consider both natal and breeding dispersal

behaviours. All focal species are closely related and fall within similar weight and size classes (Poole, 2005). As dispersal generally scales with body size (Thornton & Fletcher, 2014), the dispersal model was parameterized similarly across all species. The dispersal model was initialized using current observations of each species and was run using three time steps, current (2000), 2050s and 2080s, reflecting future climate projections. Mapped projections were converted to binary presence/absence data using a threshold maximizing the True Skill Statistic (Allouche *et al.*, 2006). I replicated the dispersal simulation model a total of 20 times for each unique combination of species × seasonal range × SDM technique × GCM. The final dispersal restricted distributions were based on a consensus across all replicates where any cell considered colonized in any one replicate was retained in the final consensus output representing occupied suitable habitat in the 2080s.

2.3.5   Variable importance

In addition to comparisons of predictive accuracy across the three variable sets, I investigated the relative importance of predictor variables based on the final calibrated model for each species, across all each model algorithm, variable set and seasonal distribution. I applied a permutation test that is independent of modeling algorithm thus allowing direct comparisons between alternative models. For all possible combinations across the factorial design, the importance of each variable was assessed within biomod2 whereby predictions are compared between the original fitted values and against predictions where each predictor was randomly permuted in turn (Thuiller *et al.*, 2009). Low correlations between predictions indicate which variables are relatively important as indicated by a high degree of dissimilarity between predictions when that variable is permuted. This procedure was repeated 100 times and an average correlation coefficient was calculated. The final metric is expressed on a scale from zero to one where a higher value reflects a more influential predictor.

2.3.6　Projected shifts in species distributions

To measure predicted impacts of future climate change on species distributions, I calculated multiple metrics between current and future predictions (2080). The metrics characterize different properties of range dynamics over space and time and as such provide a multi-dimensional perspective on patterns of range shift. As a measure of change in distributional area, for each species, season, variable set, modelling algorithm, and GCM, I calculated the proportional change in range size between the current predicted and 2080 projections. This metric is standardized across species; a value of 1 represents no change in range area: a value less than 1 corresponds to declines, and a value greater than one represents increases. To measure both distance and direction of shift, the difference in range centroids, based on mean latitude and longitude across all binary cells predicted as present, was calculated between the current period and the 2080s. Finally, I calculated the relative change in the northern and southern range boundary positions where boundaries were delineated based on the mean latitude position of 2.5% (northern) and 97.5% (southern) of all grid cells predicted as suitable and colonized for each time period of analysis. Quantifying distributional shifts in range boundary positions based 2.5% of all predicted cells reduced the influence of outliers (Comte & Grenouillet, 2013). All assessments were undertaken on dispersal-mediated binary mapped predictions. Distances and directions were calculated using the geosphere R package (Hijmans, 2014). All other calculations were undertaken using R. 2.15.3 (R Core Team, 2013).

2.3.7　Statistical analyses

Model performance based on AUC, TSS, and BCC among the three variable sets was assessed using a Wilcoxon rank signed test. ANOVA was used to evaluate the sensitivity of two metrics of range shift to multiple sources of uncertainty. The metrics evaluated included relative change in range size and relative change in northern and southern range margin boundaries. I performed a four-way ANOVA without replication (Sokal & Rohlf, 1995) using variable set, model algorithm (SDM), GCM, and species identity as the fixed factors. As a consequence of no replication, it was not possible to estimate variance

associated with the 4-way interaction of the fixed factors (Sokal & Rohlf, 1995), and I did
not include species in the interaction to focus on the manipulated sources of variation. For
each ANOVA, I calculated the effect size for variable set, model algorithm, GCM,
species identify, and their interactions to determine the relative strength of the
relationship between each factor and the variance of the response variable. For each
factor, the effect size (eta^2) was calculated as the ratio of the effect variance (factor sum
of squares, SS) to the total variance (total SS) (Tabachnick & Fidell, 2007). All range
shift metrics were assessed for normality using the Anderson-Darling test and square root
and log transformations were applied when assumptions were violated. The southern
range boundary shift could not be normalized following transformations, thus I omitted it
from the statistical test, and instead compared it qualitatively to other range shift metrics.
All modeling and analyses were performed R version 2.15.3 (R Core Team, 2013). Linear
mixed models (LMMs) were performed for comparison and included three fixed factors:
variable set, model algorithm, and GCM, and species identity was modeled as a random
effect. LMMs were performed using the '*lme4*' and '*car*' R packages (Fox & Weisberg,
2011, Bates *et al.*, 2013). R^2 calculations of the mixed models followed methods in
(Nakagawa & Schielzeth, 2013) and were implemented using the R package "*MuMIn*"
(Barton, 2013).

2.4   Results

2.4.1   Predictive accuracy

Predictive accuracy metrics were sensitive to the seasonal distribution under
consideration and to the inclusion of biotic habitat variables (Fig. 2.7.1). Across the three
variable sets, breeding season models tended to outperform nonbreeding models based on
all three metrics, AUC, TSS, and COR, when averaged across the species. Mean
predictive accuracy increased with the inclusion of habitat-based predictor variables
across both seasonal ranges, except for TSS of the nonbreeding range. Differences in
AUC and TSS between climate-habitat and climate-only models for each seasonal range
were not significant, although overall variation between the variable sets was reduced
when habitat factors were included (Wilcoxon signed test: $p > 0.05$; Fig. 2.7.1). However,

pair-wise COR values were on average higher for climate-habitat models relative to climate only models (Wilcoxon signed test: $p > 0.05$). Based on AUC scores, both breeding and nonbreeding season habitat-only models were fair, with mean values falling between $0.7 \leq AUC \geq 0.8$, and climate-only and climate-habitat models were considered excellent ($0.9 \leq AUC$) (Swets, 1988). Across both seasonal distributions, habitat-only models resulted in significantly lower predictive accuracy scores for the three metrics based on paired-comparisons between both climate-only and climate-habitat model metrics (Wilcoxon signed test: $p < 0.001$, in all comparisons). As habitat-only model predictive performance was particularly low and mapped predictions exhibited large discrepancies compared to the climate-only and climate-habitat models, habitat-only models were not considered in subsequent analyses.

2.4.2   Variable importance

The relative importance of predictors varied across seasonal distributions, suggesting differences in environmental variables responsible for structuring species seasonal ranges. Based on permutation measures of variable importance across the climate-habitat models and summarized across all models and species, climate variables were on average more important than variables describing habitat and land use-land cover diversity for both seasonal distributions (Fig. 2.7.2). Among the four climate variables, the mean rank of each differed as a function of the seasonal distribution under consideration. For breeding distributions, maximum temperature and cumulative precipitation were the two most important, while for nonbreeding distributions, temperature seasonality followed by maximum temperature were the two top-ranked variables, in decreasing order of importance. The relative rank of climate predictors was generally consistent when compared with climate-only permutation variable importance outcomes (Fig. 2.8.1). Across both seasonal distributions, biotic vegetation variables and land-use land-cover diversity were on average ranked lowest in importance, across all species. Biotic vegetation factors tended to be more influential across nonbreeding seasonal distributions compared to the breeding season. Despite the relatively low mean importance of biotic variables, for a subset of species biotic factors outranked abiotic predictors in terms of

permutation importance, a pattern especially evident across nonbreeding models (Fig. 2.7.3). Furthermore, composite maps of species richness between the two variable sets revealed spatially structured differences in predicted outputs (Fig. 2.7.4). In the nonbreeding range, climate-only models tended to predict higher richness in regions of high topographic complexity. Spatial patterning of differences was more complex in the breeding season, where spatial heterogeneity was most prominent around range margins. Climate-habitat predictions resulted in fine-scale differences reflecting the heterogeneity introduced by the additional predictors.

2.4.3 Sources of variation in potential range dynamics under climate change

ANOVA results for 2050 and 2080 were qualitatively similar, so I only report results for the 2080 period. Mixed-model outcomes were similar to fixed-effect models; I report the results for the fixed-effect outcomes as they include effect size measures. Mixed-effect results are found in Appendix Table 2.8.3. Across all models species identity was consistently significant and accounted for the majority of the variation across all metrics, and I focus the remaining results on effect size comparisons among the three fixed factors. Based on fixed-effect ANOVA models, factors contributing the most to variation in relative change in range size differed depending on the seasonal range under consideration (Table 2.6.2). For both breeding and nonbreeding season change in range size (adjusted R^2 of 0.3997 and 0.2251, respectively), model algorithm had the largest effect followed by variable set, or an interaction between model algorithm and GCM, depending on the seasonal range. Predictions based on climate-only models resulted in more extreme estimates of range change on average, leading to greater projected declines in suitable area (Fig. 2.7.5). This was generally consistent regardless of the model algorithm applied, except in the case of MaxEnt models. While declines in range size are the general anticipated trend, certain combinations of model technique and variable sets led to increases in relative size, highlighting the importance of interacting effects. Variation in change in range size across the nonbreeding season was evident between GCMs, which was amplified depending on the model technique applied. This was most

apparent for models developed using GBM techniques and under NIES and CCMA-GCM3 projections (Figure 2.8.2). Similar to breeding outcomes, projected range sizes are generally expected to decline over time under climate change, however, there was substantial variation in outcomes. This was in part driven by having proportionally more species expected to undergo range expansions, which was compounded by high variability related to choice of modeling technique (Table 2.6.2, Fig. 2.7.5).

Different sets of factors disproportionately affected variation in northern range boundary shifts relative to projected change in range size, highlighting metric-specific sensitivities. Overall, GCMs accounted for most of the variation in range margin shifts (after species identity) followed by an interaction between model technique and variable set, regardless of the season under consideration (Table 2.6.2). Substantial variation in northern range margin shift appeared to be driven by two GCMs, CSIRO-MK3 and NIES-99. The dominant direction of both northern and southern range margin shifts across breeding distributions was largely in the direction of more northern latitudes. However, species-specific plots revealed variation in both directions and magnitude of predictions (Figs. 2.6.6, 2.6.7). Based on northern median centroid shifts, breeding centroids were clearly expected to shift north, albeit with variation attributed to the choice of GCMs. By comparison, both variable set and choice of GCMs were important factors affecting nonbreeding northern range margin shifts. Variation as a result of these two factors was relatively high resulting in variable magnitudes of shift in terms of distance although no clear trends in directionality of boundary shift (Figs. 2.6.6, 2.6.7). Considering the distance of range centroid shifts, there was a tendency for median range centroids to shift in a northerly direction, although the magnitude of shift was much smaller relative to breeding range centroid predictions (Fig. 2.6.8). Radial plots revealed species-specific variation in both distance and directionality and provide a more complex picture of range shifts with climate change than when focusing only on pole ward shifts and metrics summarized across all species (Fig. 2.6.9).

2.5   Discussion

Characterising and quantifying species' vulnerability includes assessment of the degree to which available suitable climate-habitat conditions persist under climate change scenarios. Despite the importance of considering all seasonal habitats required over the annual cycle when evaluating vulnerability or when aiming to understand the factors that structure species ranges, relatively few studies address annual life-cycle requirements (but see Doswald *et al.*, 2009). Here I have shown that including biotic vegetation factors improves predictive performance across both seasonal ranges for 33 Nearctic-Neotropical migratory bird species, while variation in relative importance of predictors suggests limiting factors are seasonally dependent. The inclusion of biotic factors had cascading influence on predicted range shifts, with seasonally dependent patterns of change. The sensitivity analyses carried out here on the climate change vulnerability assessments revealed that metrics describing range shift dynamics were highly sensitive to multiple factors commonly used to parameterize SDMs and predict range-wide consequences of climate change, including selection of predictor variables, model technique, and GCM. However, the role of different sources of uncertainty was not consistent between the two seasonal ranges considered and varied as a function of the metric of change. This research adds to the body of evidence emphasizing the need to systematically address the role of uncertainties in SDM outcomes in particular when considered in a decision-making context and calls for expansion of commonly used metrics of range change to consider those describing the multi-dimensionality of species' ranges over both space and time.

   The selection of biologically relevant predictor variables is a critical element in the model development process, influencing model inference and predictive performance. Based on multiple metrics of predictive accuracy, the inclusion of biotic vegetation predictors and a measure of land-use land-cover diversity improved model performance across both seasonal distributions. Models calibrated using only biotic vegetation variables performed poorly underscoring the relevance of climatic factors as important determinants of species' distributions at broad spatial extents and resolution, a result that is echoed in other studies (Luoto *et al.*, 2007, Barbet-Massin *et al.*, 2012b, Xu *et al.*,

2014). The generally poorer performance of nonbreeding models likely results from data quality issues due to lack of systematic sampling in these regions, yet, overall performance closely approximated breeding season estimates. The improvement in predictive performance with the inclusion of habitat variables suggests that these proximal variables describe important resource dependencies, here acting as surrogates for breeding requirements and food availability, and affect predicted distributions even at broad spatial scales (Austin, 2002, Wisz *et al.*, 2013). Furthermore, comparison of mapped predictive outcomes based on climate-habitat models depicted more fine-grained patterns relative to coarse appearance of climate-only models as these models are capable of capturing detailed patterns of habitat variables considered.

Importance values based on randomization of each predictor further emphasize the relative importance of abiotic factors. The clear distinction in relative importance of abiotic factors suggests seasonal limitations reflective of the seasonal climatic profiles of the temperate (breeding) versus tropical (nonbreeding) geographic regions. For example, maximum temperature is a limiting factor in the northern temperate breeding ranges, while precipitations ranked highest in the nonbreeding season, reflective of low temperature variability and higher precipitation variability that characterize the nonbreeding regions. Due to the correlative nature of the modelling framework applied, relationships are not causative, and thus it is not possible to distinguish or infer the underlying mechanism related to the focal species' distributions. Despite these known caveats of phenomenological methods, the results obtained in this study suggest an important role for biotic vegetation factors as constraints to species' distributions. That different environmental factors may be contributing to species distributions within a species across seasonal ranges presents interesting hypotheses to test related to the propensity for seasonally tracking of climate and non-climatic factors for migratory species (e.g., Marini *et al.*, 2010).

Both breeding and nonbreeding ranges were expected to decline in relative range size on average under climate change, a result that was generally consistent across the multiple sources of variation considered in the sensitivity analysis. This suggests that

these migrants may be negatively influenced by climate change across both seasonal distributions. Climate-only models resulted in more extreme and pessimistic predictions of range change relative to models incorporating biotic vegetation factors. However, the relative difference in range size and the proportion of species expected to undergo declines in range size between the two variable sets was greater for breeding season predicted changes. There are a number of possible reasons for these predicted differences. First, on average, climate-habitat models resulted in improved predictive performance and discrimination capacity regardless of the season. The inclusion of biotic vegetation variables tended to minimize the strength of abiotic climate predictors; this down weighting of abiotic effects is in part responsible for more conservative future predictions. Secondly, biotic vegetation factors were greater on average across nonbreeding models suggesting differences in limiting factors between the seasonal distributions. And finally, some of the largest temperature increases are expected in temperate regions following clear latitudinal gradients where many of the focal species breed while nonbreeding regions are likely to experience more heterogeneous changes in precipitation and some of the most novel climates (Garcia *et al.*, 2014). The northward shift of breeding range centroids mirrors the large velocity and directional climate changes expected in high latitude regions (Loarie *et al.*, 2009), however, the distance shifts were not of similar magnitude between seasons, potentially resulting in increased migration distances. Increased migration distance may equate to increased energetic requirements necessitating increased time spent feeding either before or during migration; this has the potential to elevate the vulnerability of long-distance migrants to potential climate change (Doswald *et al.*, 2009).

In this study, the relative importance of different sources of variation was dependent on the metric used to measure range shifts. Model algorithm and GCMs had the highest effect sizes (after species identity) on relative change in range size and shift in northern range boundaries, respectively. Previous studies have generally found that model algorithm followed by GCMs contribute the most to uncertainties in future range shifts (Diniz-Filho *et al.*, 2009, Buisson *et al.*, 2010, Lemes & Loyola, 2013), although the

proportion of variance explained between the two factors tends to balance each other based on later versus mid-century projections (i.e., 2080 vs 2050) (Buisson *et al.*, 2010). However, the previous studies generally focused on a singular metric of range change, in particular species richness, or change in range size. The research presented here suggests that general conclusions on the major sources of variation are likely context-specific, and dependent on the measure of range change. While I have only focused on two measures, they were selected as they measure distinct properties of range shift: size and extreme range margins. Considering multiple metrics provides a more complete picture of the heterogeneity and complexity of species' distributional responses due to climate change (Grenouillet & Comte, 2014). While a diversity of metrics can capture geographical complexity of range shifts, assessing their sensitivity to multiple sources of uncertainty particularly when used to assess predictions under climate change is required for robust interpretations.

Knowledge of the relative importance of various sources of uncertainty can provide guidance on how to address uncertainties and reduce variability in projected outcomes. At its root, variation between GCMs results from multiple sources of uncertainty associated with modeling the complex climate systems, including parameterization, downscaling method, as well as temporal and spatial variations in climate model performance and ability to simulate current conditions (Beaumont *et al.*, 2008). SDM algorithms, while united by their correlative approach, can differ substantively in terms of parameterization, type (e.g., regression or machine-learning), and underlying assumptions (Elith & Graham, 2009, Dormann *et al.*, 2012). While attention and appropriate selection of model techniques should reflect criteria such as model objective, or type of data as best as possible, an increasingly common method to address these sources of variation is to develop predictions based on consensus rule (Araújo & New, 2007b). Such an approach may yield robust results when multiple SDMs or climate models are equally appropriate.

Finally, I found that the inclusion of biotic predictors accounted for non-negligible sources of uncertainty in both metrics. While SDM algorithm and GCM have garnered much attention as sources of uncertainties in vulnerability assessments to climate change

(Dormann *et al.*, 2008b, Diniz-Filho *et al.*, 2009, Buisson *et al.*, 2010), the sensitivity to model selection has received less focus. Given the increased predictive performance of models including both abiotic and biotic factors, the sensitivity of metrics to the inclusion of biotic vegetation factors could reflect errors arising from misspecified models. This reinforces the need to consider predictor selection to reflect biologically-relevant constraints (Iverson & Prasad, 1998, Austin, 2002, Austin & Van Niel, 2011). While many additional factors contribute to species' propensity to track climate change, limits will in part be determined by the availability of habitat features, such as biotic vegetation components, consequently these features should not be ignored from range-wide scale analyses.

I considered biotic vegetation variables as static in nature, and so interpretation of the outcomes needs to be reflected by the limiting assumption that they remain temporally invariant. Changes in land-use and land-cover change are expected to have far-reaching consequences on biodiversity, in particular within tropical regions (Jetz *et al.*, 2007). While the inclusion of biotic factors improved predictive performance and it has been suggested that they be considered essential when the goal is to predict range shifts under climate change (Stanton *et al.*, 2012), given that habitat loss is likely to remain a pervasive threat into the future, predicted changes are likely underestimated. Further under- or over-estimation in relative risks are likely given the absence of demographic processes that actually drive range changes. These results clearly demonstrate that there is substantive variation in predicted range margin shifts among species, and in relation to model uncertainties. Range margins are important parts of a species' distribution as individuals from margin populations are likely drivers of actual range shifts through colonization and extinction processes. SDM predictions may result in spatially structured errors due to different processes dominating at leading vs lagging range margins (Hampe & Petit, 2005) that are likely amplified when demographic processes are not accounted for (Naujokaitis-Lewis *et al.*, 2013). During the nonbreeding season, the range size of Nearctic-Neotropical migratory birds is generally smaller than during breeding season. Not only does this result in higher densities of long-distance migrants, but they often co-

occur in mixed-species flocks with both resident species and other long-distance migrants where inter-specific competition may plan an important role in structuring avian communities (Jankowski *et al.*, 2010). The consequences of climate change on biotic interactions in these tropical communities where Nearctic-Neotropical migrants spend the majority of their life-cycle is a particularly important research gap (Şekercioğlu *et al.*, 2012), especially given the importance of biotic interactions as mediators of climate influence relative to direct abiotic mechanisms (Ockendon *et al.*, 2014).

Long-distance migratory birds spend different portions of their life-cycle in regions characterized by largely different environmental conditions; these results demonstrate how climate change is likely to act independently on seasonal ranges resulting in predicted declines in range size and asymmetric magnitude of directional changes. By addressing potential climate change impacts across both seasonal ranges, this work extends previous assessments constrained to a singular portion of the annual cycle (Jetz *et al.*, 2007, Huntley *et al.*, 2008, Doswald *et al.*, 2009). This reveals a comprehensive picture of vulnerabilities based on predicted responses to climate change. These results underscore the following points: (1) omission of biotic vegetation variables results in reduction of predictive accuracy, (2) relative importance of abiotic and biotic covariates varies as a function of the season under consideration, (3) missing covariates had cascading influences on projections of range shift under climate change suggesting that both climate and habitat vegetation limit species' distributions, and (4) range shift metrics were not equally sensitive to multiple sources of uncertainty. I contend that projected impacts of climate change on range shifts requires evaluation of habitats required across the annual cycle, and comprehensive quantification of uncertainty on metrics of range change. An appreciation of the multi-dimensionality of predicted range shifts alongside systematic evaluation of their sensitivity to multiple sources of uncertainty will enable more informed vulnerability assessments.

2.6 Tables

Table 2.6.1 Three predictor variable sets used to model *Parulidae* species breeding and nonbreeding distributions. Habitat-only: biotic vegetation factors, climate-only: abiotic factors, and climate-habitat: a combination of both abiotic and biotic factors.

	Habitat-only	Climate-habitat	Climate-only
Temperature seasonality (100 * SD)		X	X
Precipitation seasonality (CV)		X	X
Nonbreeding /breeding cumulative precipitation			X
Nonbreeding /breeding maximum temperature			X
Proportion forest cover	X	X	X
Proportion shrub cover	X	X	X
Number of vegetation land-cover classes	X	X	X

Table 2.6.2 Summary statistics of fixed-effect ANOVAs of (A) relative change in range size and (B) relative change in northern range margin position. Range margins were calculated based on 2.5% quantiles of all cells predicted as suitable. *P*-values are indicated as follows: $p < 0.001$ by ''***'', $p < 0.01$ by ''**'', $p < 0.05$ by ''*'', ''NS''are non-significant values. GCM: General Circulation Model, SDM: Species Distribution Model.

Metric	Factor	Breeding			Nonbreeding		
		F	Sig	Effect size (Rank)	*F*	Sig	Effect size (Rank)
(A) Range size	Variable set	59.26	***	0.034 (3)	0.59	NS	0.001
	GCM	12.70	***	0.022 (4)	0.98	NS	0.003
	SDM	23.34	***	0.040 (2)	20.89	***	0.041 (2)
	Species	17.28	***	0.315 (1)	6.57	***	0.206 (1)
	Variable set:GCM	0.23	NS	0.000	0.54	NS	0.002
	Variable set:SDM	10.10	***	0.017	3.14	*	0.006 (4)
	GCM:SDM	0.58	NS	0.003	2.57	*	0.015 (3)
	Adjusted R^2	0.3997			0.2251		
(B) North range margin	Variable set	1.56	NS	0.001	8.18	**	0.007 (4)
	GCM	99.51	***	0.129 (2)	6.93	***	0.017 (2)
	SDM	5.13	**	0.007 (4)	0.32	NS	0.001
	Species	30.30	***	0.418 (1)	13.60	***	0.357 (1)
	Variable set:GCM	0.55	NS	0.001	0.08	NS	0.000
	Variable set:SDM	6.86	***	0.009 (3)	4.45	*	0.007 (3)
	GCM:SDM	1.06	NS	0.004	0.42	NS	0.002
	Adjusted R^2	0.5448			0.3509		

Table 2.6.3 Percentage of species (*n*=33) projected to increase or decrease in median range size across four GCMs to the 2080s by seasonal range for SDMs using climate-only variables and climate-habitat variables.

| Season | Variable set | Direction of change | GCM | | | | Mean across GCMs |
			CCMA-GCM3	CSIRO-MK3	Hadley	NIES-99	
Breeding	Climate	Decrease	88 %	80 %	86 %	92 %	86.5 %
	Climate	Increase	12 %	20 %	14 %	8 %	13.5 %
	Climate-habitat	Decrease	77 %	66 %	77 %	80 %	75 %
	Climate-habitat	Increase	23 %	34 %	23 %	20 %	25 %
Nonbreeding	Climate	Decrease	70 %	72 %	78 %	72 %	73 %
	Climate	Increase	30 %	28 %	22 %	28 %	27 %
	Climate-habitat	Decrease	65 %	69 %	75 %	71 %	70 %
	Climate-habitat	Increase	35 %	31 %	25 %	29 %	30 %

2.7   Figures
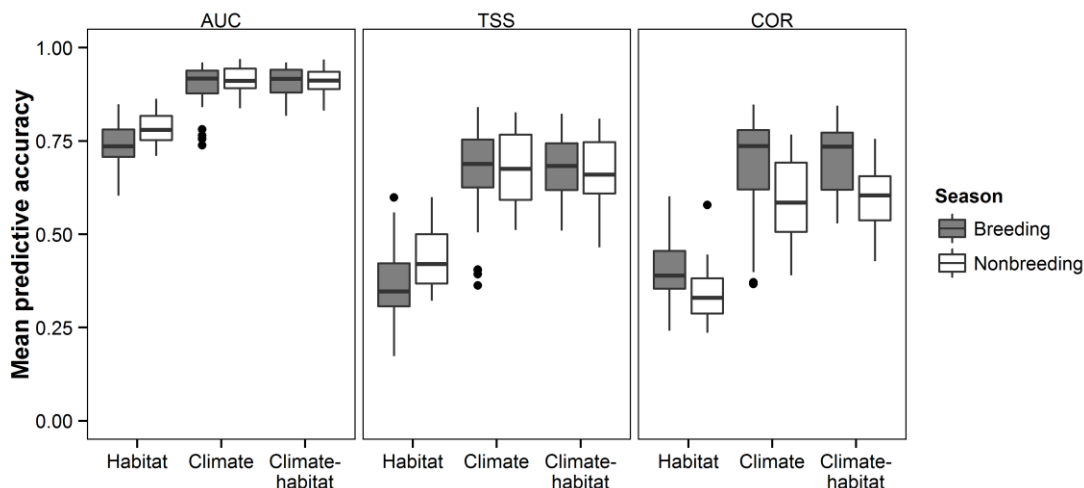
Figure 2.7.1 Variation in mean predictive accuracy measures averaged across distribution models based on three sets of variables describing: (1) habitat, (2) climate, and (3) both climate and habitat for 33 species of *Parulidae*. Results are compared between models developed independently for the breeding and nonbreeding seasons. Boxes represent median, first and third quartiles; the whiskers depict the interquartile range × 1.5 with outliers are included. AUC: area under the receiver operating characteristic curve, TSS: true skill statistic, COR: point biserial correlation.
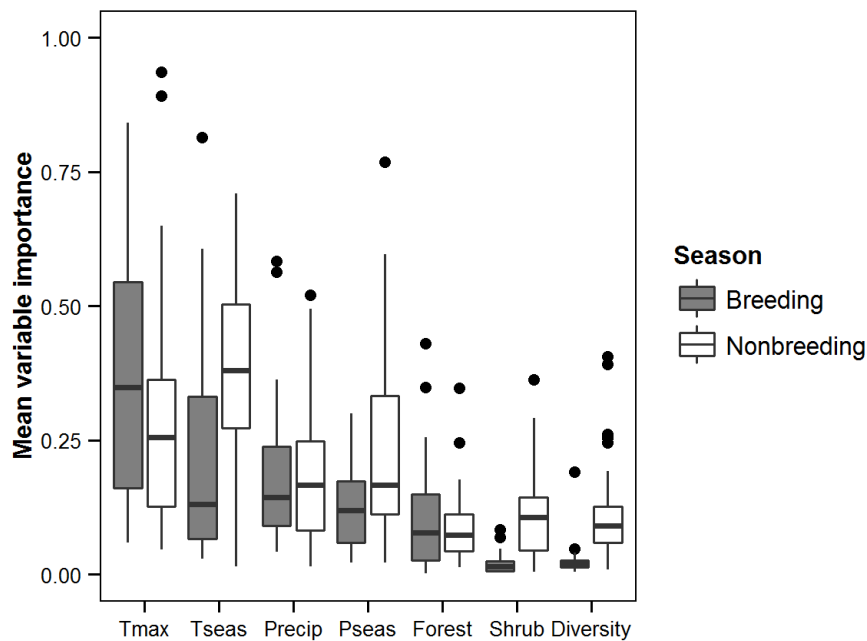
Figure 2.7.2 Mean permutation variable importance averaged across five model algorithms based on models calibrated with the climate and habitat variables across the breeding and nonbreeding seasons for 33 *Parulidae* species. Predictors include abiotic variables of Tmax: seasonal mean of the maximum temperature, Tseas: temperature seasonality, Precip: seasonal cumulative precipitation, Pseas: precipitation seasonality, followed by biotic vegetation associations. Boxes represent median, first and third quartiles; the whiskers depict the interquartile range × 1.5, and outliers are included.
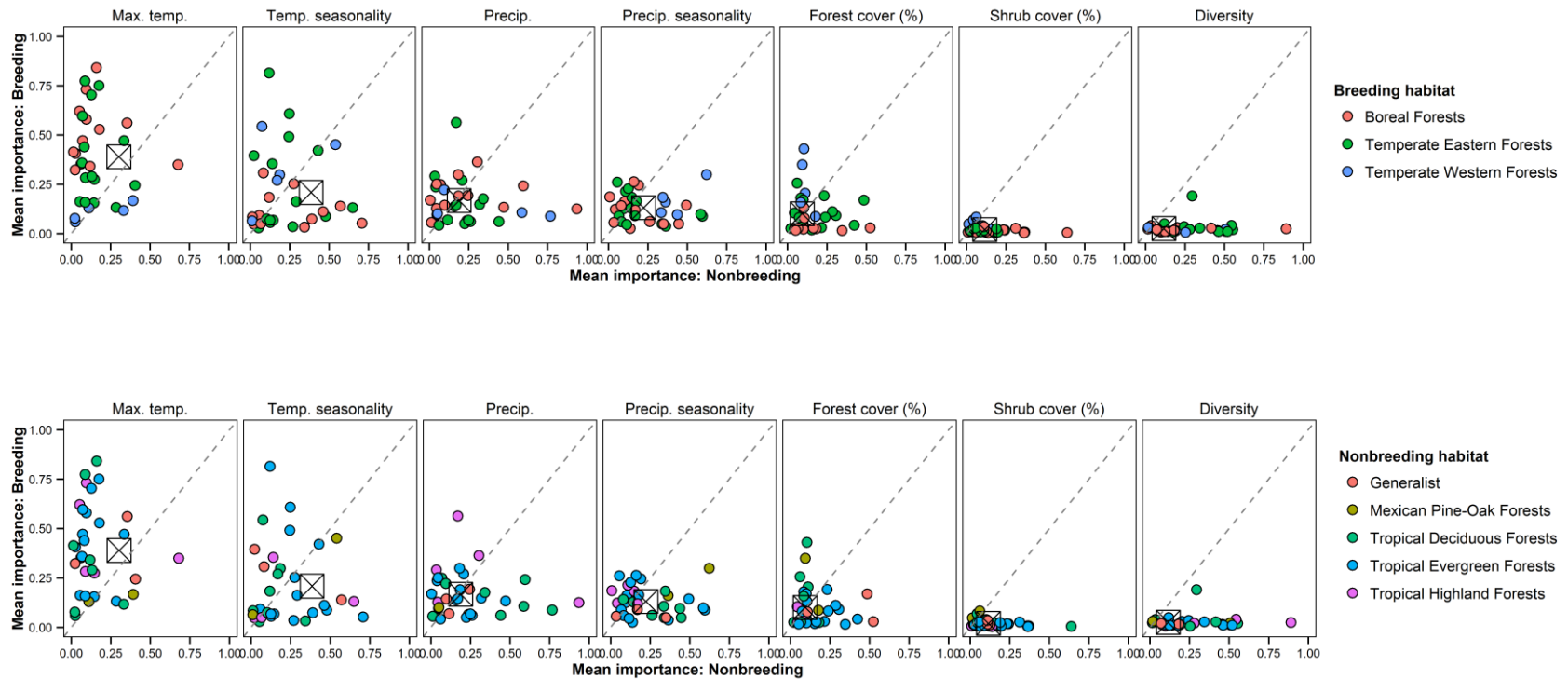
Figure 2.7.3 Mean permutation importance of nonbreeding relative to breeding predictions for 33 species of Parulidae. A higher importance value denotes a more influential predictor in the model. Colours reflect dominant habitat preferences on the breeding grounds (top) and nonbreeding grounds (bottom) following Berlanga *et al.* (2010). '□' represents the mean importance value across all species and model algorithms for each variable.
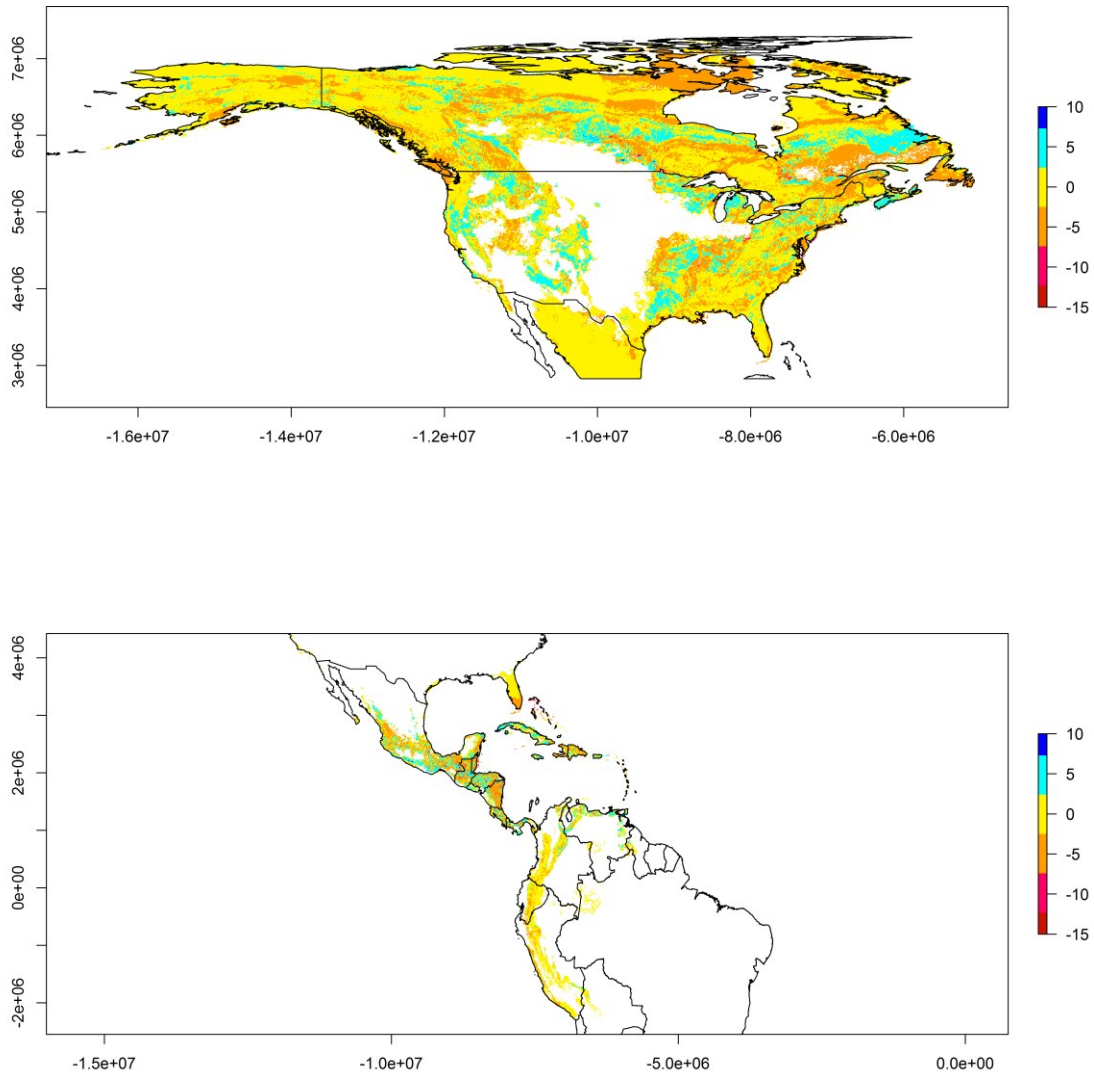
Figure 2.7.4 Difference maps of predicted species richness (out of 33 species) based on stacked single-species model outcomes between climate-only and climate-habitat model predictions for breeding season (top) and nonbreeding season (bottom) distributions. Climate-habitat species richness predictions were substrated from climate-only maps; negative values indicate higher predicted overall richness of climate-habitat models.
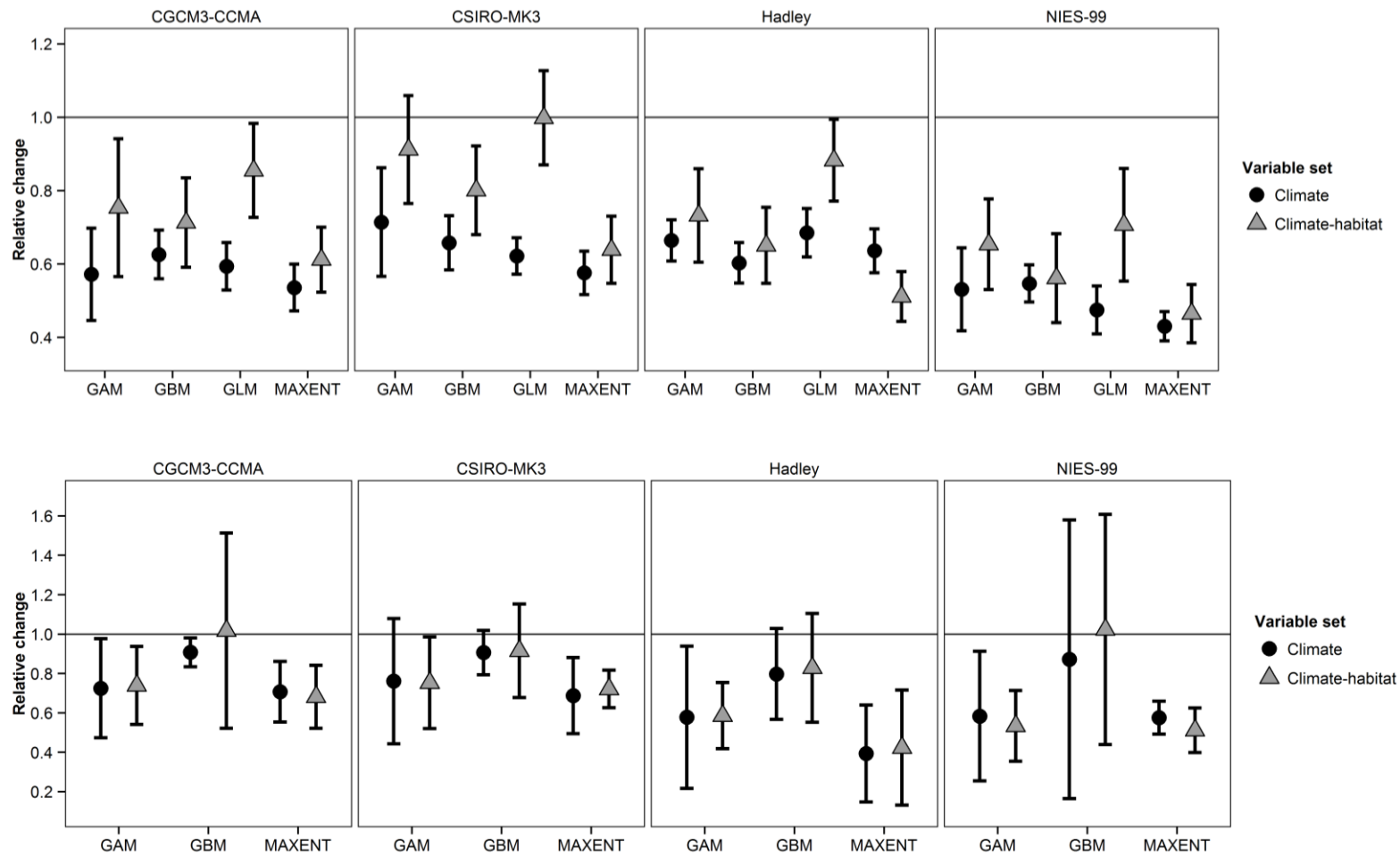
Figure 2.7.5 Variation in potential relative change in range size between current predictions and 2080s projections in relation to three factors: variable set, modeling technique, and general circulation model. Values are based on median change and bars represent standard errors across all species for the breeding (top) and nonbreeding (bottom) seasons.
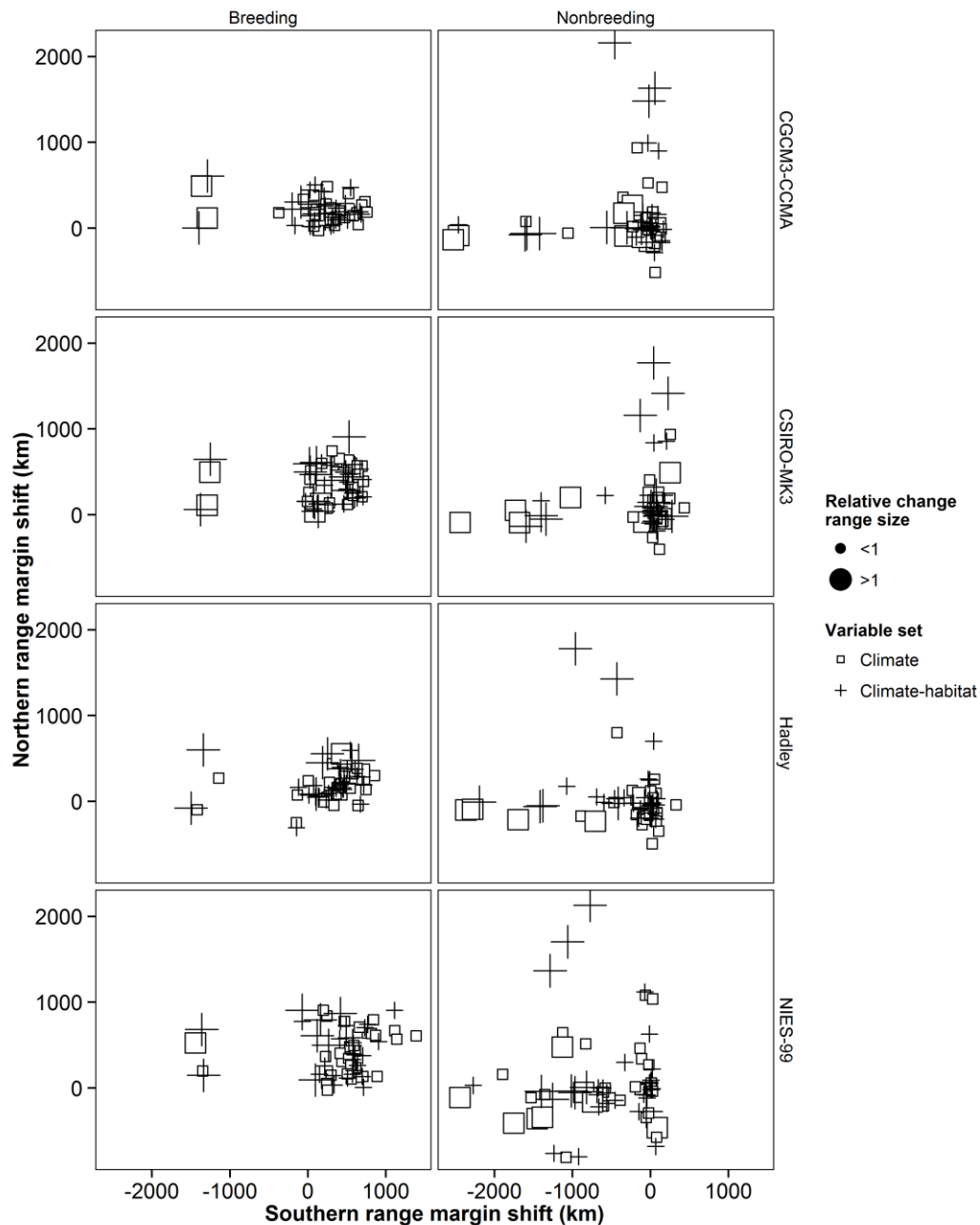
Figure 2.7.6 Variation in predicted median northern and southern range margin shifts under climate change to the 2080s under four general circulation models and two variable sets, climate-only and climate-habitat. Results are contrasted between breeding and nonbreeding ranges for each species where points are scaled to represent relative change in range size. <1 indicates a decline in range size and >1 an increase over time.
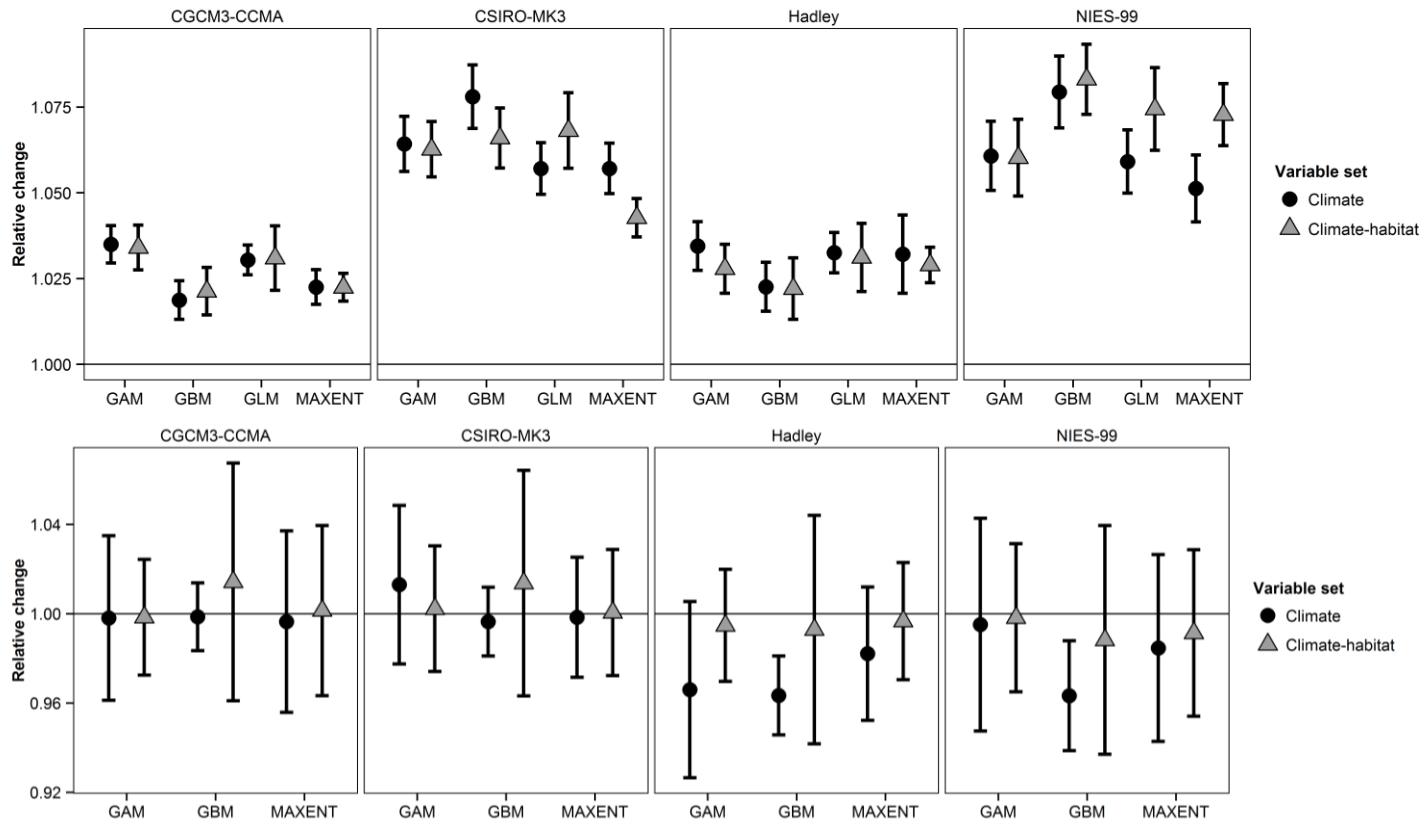
Figure 2.7.7 Variation in relative change in northern range boundary position between current and 2080s predictions in relation to three factors: variable set, modeling technique, and general circulation model. Values are based on median change and bars represent standard errors across all species for the breeding (top) and nonbreeding (bottom) seasons
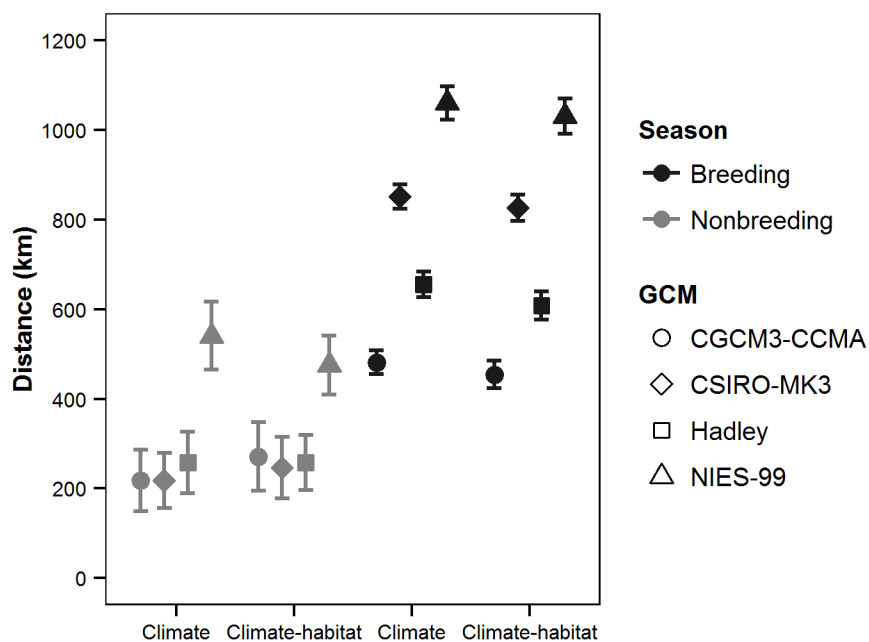
Figure 2.7.8 Median projected shift north of range centroids (km) between current and 2080s projections for 33 species of *Parulidae* and summarized across five modelling techniques. Variations are contrasted between seasonal distributions; two variable sets, climate-only and climate-habitat; for four GCMs. Bars represent standard deviations estimated across the 33 species modeled.
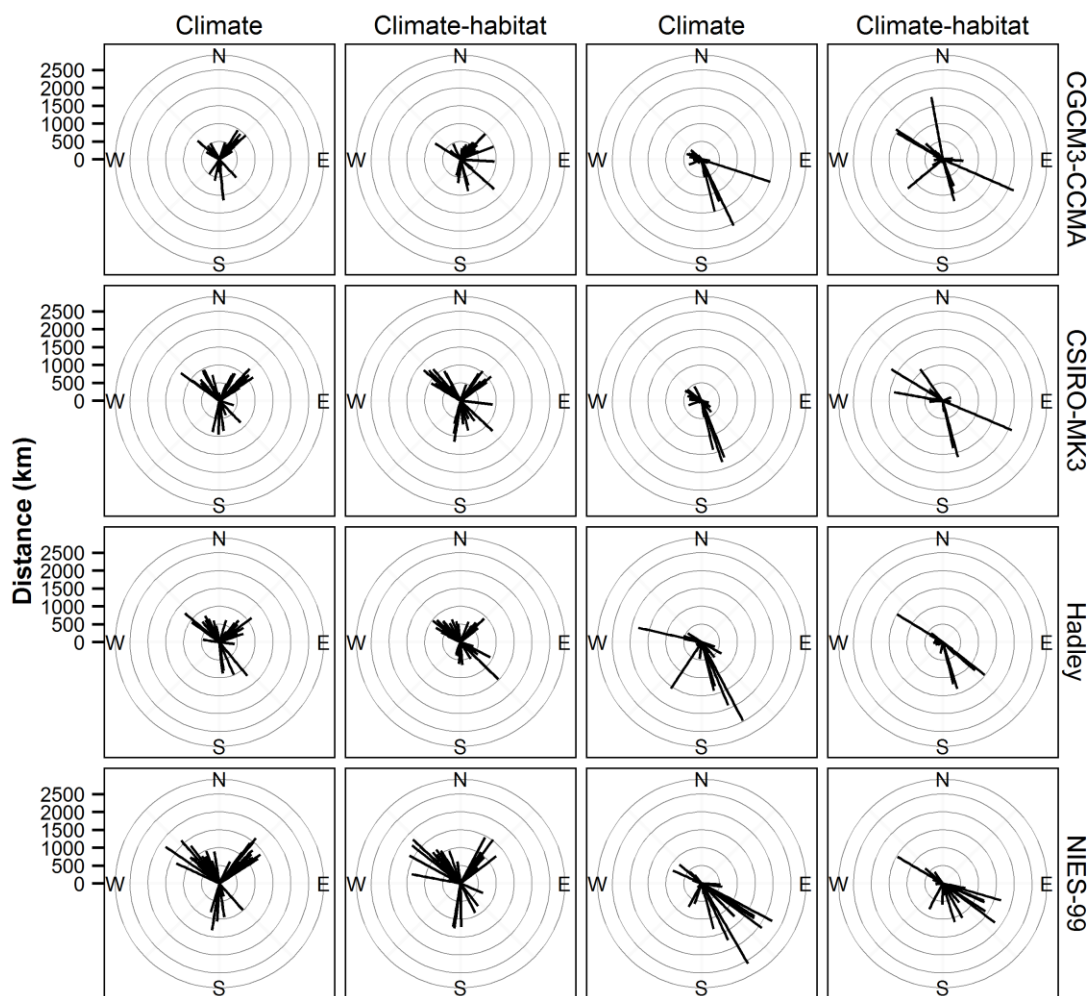
Figure 2.7.9 Difference in median directional changes in range centroids under climate change to the 2080s for each species by seasonal range across four general circulation models. Distance and direction are summarized based on the median across five modeling techniques and contrasted between variable sets (climate and climate-habitat) for the breeding (1st two left-hand columns) and nonbreeding (last two right-hand columns) seasons.

2.8 Appendix

2.8.1 Tables

Table 2.8.1 Description of focal species from the family *Parulidae* assessed in Chapter 1, including habitat preferences and life-history traits compiled from (Poole, 2005, Berlanga *et al.*, 2010). Species alpha codes (abbreviations) follow the four-letter naming convention following (Pyle & DeSante, 2014).

Common Name	Latin name	Breeding habitat	Nonbreeding habitat	Feeding guild	Nest position	Median clutch size	Abbreviation
American Redstart	*Setophaga ruticilla*	Temperate Eastern Forests	Tropical Evergreen Forests	foliage gleaner	Supported	3	AMRE
Black-and-white Warbler	*Mniotilta varia*	Boreal Forests	Tropical Evergreen Forests	bark forager	Ground	5	BAWA
Bay-breasted Warbler	*Setophaga castanea*	Boreal Forests	Tropical Evergreen Forests	foliage gleaner	Supported	5	BBWA
Blackburnian Warbler	*Setophaga fusca*	Boreal Forests	Tropical Highland Forests	foliage gleaner	Supported	4.5	BLBW
Blackpoll Warbler	*Setophaga*	Boreal Forests	Tropical	foliage	Supported	4	BLPW

Common Name	Latin name	Breeding habitat	Nonbreeding habitat	Feeding guild	Nest position	Median clutch size	Abbreviation
	striata		Deciduous Forests	gleaner			
Black-throated Blue Warbler	*Setophaga caerulescens*	Temperate Eastern Forests	Tropical Deciduous Forests	foliage gleaner	Supported	4	BTBW
Black-throated Green Warbler	*Setophaga virens*	Temperate Eastern Forests	Tropical Evergreen Forests	foliage gleaner	Supported	4.5	BTNW
Black-throated Gray Warbler	*Setophaga nigrescens*	Temperate Western Forests	Tropical Deciduous Forests	foliage gleaner	Supported	4.48	BTYW
Blue-winged Warbler	*Vermivora pinus*	Temperate Eastern Forests	Tropical Evergreen Forests	foliage gleaner	Ground	5.5	BWWA
Canada Warbler	*Cardellina canadensis*	Boreal Forests	Tropical Highland Forests	foliage gleaner	Ground	4	CAWA
Cerulean Warbler	*Setophaga cerulea*	Temperate Eastern Forests	Tropical Highland	foliage gleaner	Supported	4	CEWA

Common Name	Latin name	Breeding habitat	Nonbreeding habitat	Feeding guild	Nest position	Median clutch size	Abbreviation
			Forests				
			Tropical				
Cape May Warbler	*Setophaga tigrina*	Boreal Forests	Deciduous Forests	foliage gleaner	Supported	6.5	CMWA
			Tropical				
Chestnut-sided Warbler	*Setophaga pensylvanica*	Temperate Eastern Forests	Evergreen Forests	foliage gleaner	Supported	4	CSWA
			Tropical				
Golden-winged Warbler	*Vermivora chrysoptera*	Temperate Eastern Forests	Highland Forests	foliage gleaner	Ground	5	GWWA
Hermit Warbler	*Setophaga occidentalis*	Temperate Western Forests	Mexican Pine-Oak Forests	foliage gleaner	Supported	4	HEWA
			Tropical				
Hooded Warbler	*Setophaga citrina*	Temperate Eastern Forests	Evergreen Forests	foliage gleaner	Supported	3.5	HOWA
			Tropical				
Kentucky Warbler	*Geothlypis formosus*	Temperate Eastern Forests	Evergreen Forests	ground forager	Ground	4.5	KEWA
Louisiana	*Parkesia*	Temperate	Tropical	ground	Ground	5	LOWA

Common Name	Latin name	Breeding habitat	Nonbreeding habitat	Feeding guild	Nest position	Median clutch size	Abbreviation
Waterthrush	*motacilla*	Eastern Forests	Evergreen Forests	forager			
Magnolia Warbler	*Setophaga magnolia*	Boreal Forests	Tropical Evergreen Forests	foliage gleaner	Supported	4	MAWA
MacGillivray's Warbler	*Geothlypis tolmiei*	Temperate Western Forests	Tropical Deciduous Forests	foliage gleaner	Supported	4.5	MGWA
Mourning Warbler	*Geothlypis philadelphia*	Boreal Forests	Tropical Highland Forests	foliage gleaner	Ground	4	MOWA
Nashville Warbler	*Oreothlypis ruficapilla*	Boreal Forests	Tropical Deciduous Forests	foliage gleaner	Ground	4.5	NAWA
Northern Parula	*Setophaga americana*	Temperate Eastern Forests	Tropical Deciduous Forests	foliage gleaner	Supported	4.5	NOPA
Northern Waterthrush	*Parkesia noveboracen*	Boreal Forests	Tropical Evergreen	ground forager	Ground	4.5	NOWA

Common Name	Latin name	Breeding habitat	Nonbreeding habitat	Feeding guild	Nest position	Median clutch size	Abbreviation
	sis		Forests				
Ovenbird	*Seiurus aurocapilla*	Temperate Eastern Forests	Tropical Evergreen Forests	ground forager	Ground	4.5	OVEN
Palm Warbler	*Setophaga palmarum*	Boreal Forests	Generalist	ground forager	Ground	4.5	PAWA
Prairie Warbler subsp discolor	*Setophaga discolor subspecies discolor*	Temperate Eastern Forests	Generalist	foliage gleaner	Supported	3.5	PRAW
Prothonotary Warbler	*Protonotaria citrea*	Temperate Eastern Forests	Tropical Evergreen Forests	bark forager	Cavity	5.5	PROW
Tennessee Warbler	*Oreothlypis peregrina*	Boreal Forests	Tropical Evergreen Forests	foliage gleaner	Ground	5.5	TEWA
Townsend's Warbler	*Setophaga townsendi*	Temperate Western Forests	Mexican Pine-Oak Forests	foliage gleaner	Supported	4	TOWA
Virginia's Warbler	*Oreothlypis*	Temperate	Tropical	ground	Ground	4	VIWA

Common Name	Latin name	Breeding habitat	Nonbreeding habitat	Feeding guild	Nest position	Median clutch size	Abbreviation
	virginiae	Western Forests	Deciduous Forests	forager			
Worm-eating Warbler	*Helmitheros vermivorus*	Temperate Eastern Forests	Tropical Evergreen Forests	foliage gleaner	Ground	5.5	WEWA
Wilson's Warbler	*Cardellina pusilla*	Boreal Forests	Generalist	foliage gleaner	Ground	4.5	WIWA

Globcover re-classification for land-use land-cover covariates

I reclassified the Globcover data set to a binary layer comprised of forest and non-forest by grouping 7 broad forest cover categories, including woody tree categories (40, 50, 60, 70, 90, 100, 110) and two forested wetland categories (160, 170). The percent cover of trees was then calculated for each 10 km 2 pixel. An anthropogenic category included 11, 14, 20, 30, 190. grass-shrub 120, 130, 140, 180.

Table 2.8.2 Reclassification categories of the original GlobCover (300 m resolution) dataset to derive percent forest cover, percent shrub-grassland cover, and diversity of landuse-landcover types.

GlobCover Value	GlobCover global legend	Reclassified category
11	Post-flooding or irrigated croplands	Anthropogenic
14	Rainfed croplands	Anthropogenic
20	Mosaic Cropland (50-70%) / Vegetation (grassland, shrubland, forest) (20-50%)	Anthropogenic
30	Mosaic Vegetation (grassland, shrubland, forest) (50-70%) / Cropland (20-50%)	Anthropogenic
40	Closed to open (>15%) broadleaved evergreen and/or semi-deciduous forest (>5m)	Forest
50	Closed (>40%) broadleaved deciduous forest (>5m)	Forest
60	Open (15-40%) broadleaved deciduous forest (>5m)	Forest

GlobCover Value	GlobCover global legend	Reclassified category
70	Closed (>40%) needleleaved evergreen forest (>5m)	Forest
90	Open (15-40%) needleleaved deciduous or evergreen forest (>5m)	Forest
100	Closed to open (>15%) mixed broadleaved and needleleaved forest (>5m)	Forest
110	Mosaic Forest/Shrubland (50-70%) / Grassland (20-50%)	Forest
120	Mosaic Grassland (50-70%) / Forest/Shrubland (20-50%)	Shrub
130	Closed to open (>15%) shrubland (<5m)	Shrub
140	Closed to open (>15%) grassland	Other
150	Sparse (>15%) vegetation (woody vegetation, shrubs, grassland)	Shrub
160	Closed (>40%) broadleaved forest regularly flooded - Fresh water	Forest
170	Closed (>40%) broadleaved semi-deciduous and/or evergreen forest regularly flooded - Saline water	Forest
180	Closed to open (>15%) vegetation (grassland, shrubland, woody vegetation) on regularly flooded or waterlogged soil - Fresh, brackish or saline water	Shrub
190	Artificial surfaces and associated areas (urban areas >50%)	Anthropogenic
200	Bare areas	Other
210	Water bodies	Other
220	Permanent snow and ice	Other

Table 2.8.3 Summary statistics of mixed-effect ANOVAs of (A) relative change in range size and (B) relative change in north range margin boundary position. Range margins were calculated based on 2.5% quantiles of all cells predicted as suitable. *P*-values are indicated as follows: : *p* <0.001 by ''***'', *p* <0.01 by ''**'', *p* <0.05 by ''*'', ''NS''are non-significant values. GCM: General Circulation Model, SDM: Species Distribution Model.

(A)	Fixed effects					Random effects			
	Factor	Chisq	Df	Pr(>Chisq)	Sig	Groups	Names	Variance	Std.Dev.
Breeding	Variable set	59.257	1	1.38E-14	***	Species	(Intercept)	0.02435	0.156
	GCM	38.1016	3	2.69E-08	***	Residual		0.04786	0.2188
	SDM	70.0137	3	4.24E-15	***				
	Variable set:GCM	0.6899	3	0.8756	NS				
	Variable set:SDM	30.2989	3	1.19E-06	***				
	GCM:SDM	5.2441	9	0.8125	NS				
Nonbreeding	Variable set	0.5935	1	0.44105	NS	Species	(Intercept)	0.04524	0.2127
	GCM	2.9519	3	0.3991	NS	Residual		0.19506	0.4417
	SDM	41.7761	2	8.48E-10	***				
	Variable set:GCM	1.607	3	0.6578	NS				
	Variable set:SDM	6.275	2	0.04339	*				
	GCM:SDM	15.4218	6	0.01722	*				

(B)	Fixed effects					Random effects			
	Factor	Chisq	Df	Pr(>Chisq)	Sig	Groups	Names	Variance	Std.Dev.
Breeding	Variable set	1.5553	1	0.212353	NS	Species	(Intercept)	0.000254	0.01594
	GCM	298.5256	3	< 2.2e-16	***	Residual		0.000278	0.01666
	SDM	15.3936	3	0.001509	**				
	Variable set:GCM	1.6374	3	0.65095	NS				

	Variable set:SDM	20.5799	3	0.000129	***				
	GCM:SDM	9.533	9	0.389595	NS				
Nonbreeding	Variable set	8.1827	1	0.004229	**	Species	(Intercept)	0.01019	0.101
	GCM	20.7996	3	0.000116	***	Residual		0.01941	0.1393
	SDM	0.6372	2	0.727171	NS				
	Variable set:GCM	0.2407	3	0.970764	NS				
	Variable set:SDM	8.9057	2	0.011646	*				
	GCM:SDM	2.5127	6	0.867047	NS				

Table 2.8.4 Variance explained (R^2) of mixed-effect LMMs of relative change in range size and relative change in north range margin boundary position. R^2m: marginal variance explained by fixed effects (variable set, model algorithm, and general circulation models), R^2c: conditional variance explained by both fixed and random effects (species identity).

	Metric			
	Range size		Northern range boundary	
	R^2m	R^2c	R^2m	R^2c
Breeding	0.113	0.412	0.147	0.554
Nonbreeding	0.066	0.242	0.033	0.366

2.8.2   Figures
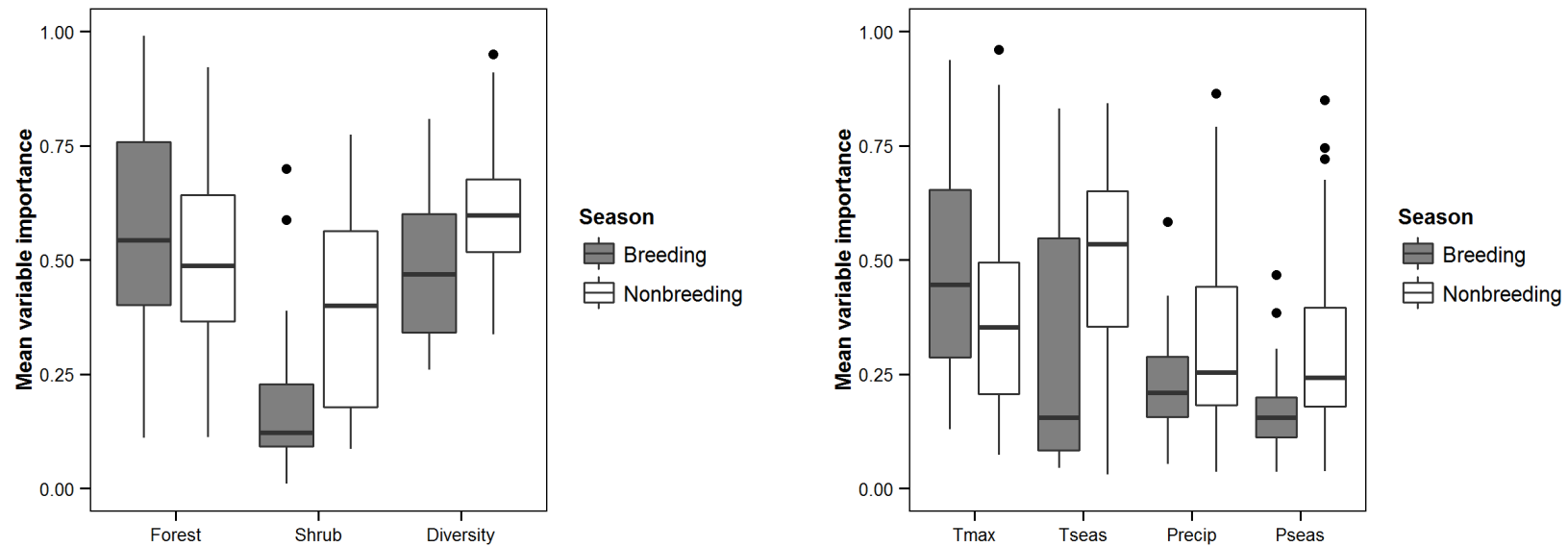
Figure 2.8.1 Mean permutation variable importance averaged across five model algorithms based on models calibrated with habitat-only variables (left) and climate-only variables (right) across the breeding and nonbreeding seasons for 33 *Parulidae* species. Predictors include abiotic variables of Tmax: seasonal mean of the maximum temperature, Tseas: temperature seasonality, Precip: seasonal cumulative precipitation, Pseas: precipitation seasonality, followed by biotic vegetation associations. Boxes represent median, first and third quartiles; the whiskers depict the interquartile range × 1.5, and outliers are included.

Deviations among GCMs: Signed standardized anomaly

To better understand which climate variables were driving the differences in future projections of suitable habitat, following (Garcia *et al.*, 2011), I assessed the deviations among GCMs during late century projections (2080s) as this is when inter-model variations within emission scenarios become most pronounced (Beaumont *et al.*, 2008). For each climate variable used in the SDM, we applied model performance metrics to distinguish between the variable for each individual GCM and the multi-model median ensemble for the same variable (Duan & Phillips, 2010). The signed standardized anomaly, *D*, is the spatially aggregated root mean square (*RMS*) difference between each individual GCM variable and the multi-model median ensemble for the same variable. *D* is standardized using the standard deviation of all GCMs. *D* reflects how much a GCM (for each variable) tends to over- or under-estimate the variable in relation to the median. *D* values close to zero indicate similarity with respect to the median.

Figure 2.8.2 *D*-metric quantified across four climate variables for 2080 projections based on four GCMs reveal contrasting deviations from median projections (gray line) by variable and seasonal range.

Chapter 3

3 Temporal variation of biotic factors underpins contemporary range dynamics of congeneric species

3.1 Abstract

Patterns of recent historical range-wide changes in species' distributions are complex often exhibiting multi-directional shifts over space and time. Long-term averages of temperature are most often used to understand such dynamic range shifts. However such a perspective may limit inferences as occupancy patterns result from a complex set of interactions between abiotic dynamics, changes in direct habitat elements, species-specific traits (thermal tolerances), and the presence of other species. Furthermore, conventional approaches to modelling species' distributions are typically snap-shots that summarize climate covariates over long-time intervals and do not account for potentially important fine-scale temporal variation in suitable habitats. I developed dynamic state-space occupancy models to test multiple competing hypotheses regarding the relative importance of major drivers of range shifts: extreme temperature, habitat, and occurrence of congeneric species, for the Golden-winged (*Vermivora chrysoptera*) and Blue-winged Warblers (*V. cyanoptera*) between 1983 and 2012. When accounting for detection errors, inter-annual variation in habitat had the strongest influence on extinction probabilities for both species with maximum temperatures ranking second or third in importance, suggesting an important role for fine-scale temporal habitat dynamics. The occurrence of the Blue-winged Warbler, a hypothesized competitor, had the largest magnitude of effect on Golden-winged Warbler extinction probability confirming anecdotal evidence of site-level species replacement. These results suggest an important role for fine-scale temporal habitat changes and the presence of congenerics on species range dynamics, challenging conventional perspectives on the lack of scaling up of biotic factors. The strength of the hierarchical modeling approach includes integration of time-dependent covariates thought to contribute to changes in population-level processes while simultaneously accounting for spatial variation in detection probabilities. As a species undergoing rapid declines and

range shifts, identifying landscapes characterised by high local extinction rates in relation to changing climates and habitat provides enhanced understanding of changes in occupancy and a platform for prioritizing conservation actions.

3.2   Introduction

Species and the systems they are found in are dynamic and understanding the factors that influence species distributions continues to be a fundamental question of ecology and evolutionary biology (Andrewarth & Birch, 1954, Gaston, 2009). While evidence of the influence of contemporary climate change on species distributions is increasing (Walther *et al.*, 2002, Parmesan & Yohe, 2003, Parmesan, 2006, Chen *et al.*, 2011b), predicting future impacts remains a complex and challenging endeavor. Species distribution models (SDMs) are a commonly employed technique to understand recent historical influences of climate change and to project future consequences on species distributions (Thomas *et al.*, 2004, Araújo & Pearson, 2005, Elith & Graham, 2009). While species-environment relationships are dynamic over space and time, traditional SDMs rely on snapshots of species occurrence data in relation to environmental factors, which limit their usefulness (Guisan & Thuiller, 2005, Franklin, 2010). Despite increasing application of temporal transferability tests to evaluate their performance in predicting observed range shifts (Rapacciuolo *et al.*, 2014), variability in SDM performance outcomes (e.g., Kharouba *et al.*, 2009, Dobrowski *et al.*, 2010, Rapacciuolo *et al.*, 2012, Schibalski *et al.*, 2014) suggests that important drivers of species range dynamics are inadequately modeled. Thus evidence increasingly fails to support the space-for-time assumption of the classic SDM framework, leading to cautionary messages both of their application to quantify extinction risk and calls for approaches that integrate population level processes that drive range dynamics (Franklin, 2010, Fordham *et al.*, 2012a, Schurr *et al.*, 2012). Given the anticipated magnitude and variability expected of global climate and land-use landcover changes (Sala *et al.*, 2000, Jetz *et al.*, 2007, Loarie *et al.*, 2009), developing a more rigorous understanding of the demographic underpinnings of range-wide dynamics over broad spatial scales and time is an imperative.

Both the space-for-time and species equilibrium assumptions of SDMs impact our understanding of range dynamics and affect their utility in applied contexts. First, the capacity for species to respond to temporally varying global changes is mediated by a combination of (1) intrinsic factors including species traits, such as dispersal, which influence vulnerability to threats (e.g., Broennimann et al., 2006, Murray et al., 2010, González-Suárez et al., 2013), and (2) the magnitude and rate of change of extrinsic conditions environmental conditions (Huntley et al., 2010). These complex dynamics and feedbacks can compromise predictive model outputs based on SDM outcomes. This can occur because species' traits can constrain demographic responses to global change leading to density dependent habitat use (i.e. use of low quality habitats as population size increases; Zurell *et al.*, 2009, Fordham *et al.*, 2013). This situation may be amplified at range edges, where species are at limits of physiological tolerances (Anderson *et al.*, 2009). Similarly, predictions based on SDMs may result in overestimation of suitable habitat under climate changes at leading edges especially where biotic factors constrain species propensity to move into climatically suitable areas (Holt, 2009, Naujokaitis-Lewis *et al.*, 2013). Secondly, predictions for species that are rapidly declining or increasing with a consequent non-stasis in range extent, or that exhibit temporal non-stationarity, may be particularly sensitive to static model assumptions (Vallecillo *et al.*, 2009, Rodhouse *et al.*, 2012). Furthermore, rates of climate and land-use-land-cover change exhibit spatial and temporal heterogeneity (Burrows *et al.*, 2014), and species responses may thus exhibit time dependent behaviors in relation to these extrinsic factors. Indeed, evidence for asymmetric range boundaries shifts and different rates of shifting range margins provides support for considering temporal dynamics of the underlying colonization and extinction events (Hampe & Petit, 2005, Hitch & Leberg, 2007, Chen *et al.*, 2011c). Thus the characterization of colonization and extinction processes across species ranges and their relationship with variables representing temporal dimensions of climate and habitat change has important implications for clarifying drivers of range dynamics.

Modeling species range dynamics requires analyses that incorporate data over multiple scales. In theory, variable selection should be informed by their biological

relevance, constituting proximate factors that directly influence species distributions at appropriate spatial and temporal scales (Elith & Graham, 2009, Austin & Van Niel, 2011). While the consequences of varying spatial resolution on models of species distributions has garnered much attention (Seo *et al.*, 2009, Franklin, 2010), the scale of temporal data has often been overlooked in the literature (but see Jackson *et al.*, 2009, Reside *et al.*, 2010, Bateman *et al.*, 2012). Short-term weather and long-term climate have long been recognized as important limiting factors to species distributions (Birch, 1957, Stenseth *et al.*, 2002). Despite this recognition, models to evaluate climate-related range shifts largely use long-term climate averages (>20 years) or large-scale oceanic indices, which dampens potentially important daily and inter-annual variability (Jackson *et al.*, 2009, van de Pol *et al.*, 2013). Indeed, species are both exposed and respond to short-term weather fluctuations and punctuated extreme weather events, which can influence demographics and dynamics at species range margins (Inouye, 2000, Parmesan *et al.*, 2000, Parmesan *et al.*, 2005, Anders & Post, 2006, Bennie *et al.*, 2013). In addition, highly mobile species are capable of responding to short-term changes in resource availability (Beerens *et al.*, 2011), with some species able to track short-term temporal changes in weather patterns to capitalize on breeding and feeding opportunities, or timing of migration (Ahola *et al.*, 2004, Bennie *et al.*, 2013, Wiebe & Gow, 2013). Thus short term weather is likely to influence distributions over broad scales and informs us of conditions faced by individuals, which can have important population-level consequences (Inouye, 2000, Dybala *et al.*, 2013, van de Pol *et al.*, 2013).

Many species rely on habitats that exhibit temporal dynamics due to either natural or anthropogenic processes, which in some cases may be largely independent of climate. Despite the predominant use of abiotic factors to describe species distributions at broad scales, the inclusion of biotic habitat elements refines model outcomes to more closely reflect the area of occupancy by capturing proximate resource dependencies (Barbet-Massin *et al.*, 2012b, Naujokaitis-Lewis Chapter 2). Temporal dimensions of habitat are important for species relying on disturbance dependent or successional habitats, while anthropogenic land-use change may contribute to landscape-level changes largely independent of climate (e.g., Santika *et al.*, 2014). Consequently, it is not surprising that

incorporating temporal variability in habitat dynamics influences species distributions and models that account for such dynamics improve outcomes (Vallecillo *et al.*, 2009, Price *et al.*, 2013, Porzig *et al.*, 2014). Furthermore, models calibrated using only climate variables may bias range-change estimates in terms of magnitude, or worse, direction (Warren *et al.*, 2001, Barbet-Massin *et al.*, 2012b), underscoring the importance of their inclusion. Despite the strong ecological underpinnings that reinforce the importance of temporal dynamics of extrinsic factors, few studies consider temporal heterogeneity in both climate and habitat condition in relation to the processes of extinction and colonization that govern dynamics of entire species' ranges (but see Bled *et al.*, 2013).

Hierarchical dynamic occupancy models (MacKenzie *et al.*, 2003) offer advances over SDMs as it is possible to estimate underlying demographic parameters of extinction and colonization that drive species range dynamics (Franklin, 2010, Pagel & Schurr, 2012, Kéry *et al.*, 2013). This increases ecological realism, focuses on process rates that drive range dynamics, and the data currency is less costly because it can use time-series of detection and non-detection data (Kéry *et al.*, 2010). The autoregressive framework of dynamic occupancy models allows for the incorporation of dependence between demographic parameters and ability to incorporate temporal dependence between covariates (Royle & Dorazio, 2008). Moreover, incorporating detection probability accounts for errors associated with false absences, which can have severe consequences on estimates of species distributions (Kéry *et al.*, 2010, Sadoti *et al.*, 2013, Lahoz-Monfort *et al.*, 2014). The ability to test relative contributions of habitat and climate changes on colonization and extinction parameters separately has the potential to provide key information relevant in a management context (McMahon *et al.*, 2011). While this flexible modeling framework can accommodate time-varying covariates, most temporally dynamic occupancy models assume that external conditions are time-invariant (but see Santika *et al.*, 2014). A rigorous assessment of temporally varying species-environment relationship can inform our understanding of the association of changing aspects of threats on range dynamics, and on the constancy of these estimates over space and time.

The goal of this chapter is to advance our understanding of the relationship between spatio-temporally dynamic threats of climate change and habitat loss on species ranges dynamics. By incorporating time-varying covariates, I provide an approach for associating climate and habitat changes to demographics of extinction and colonization probabilities that ultimately drive species' range dynamics. To do so, I use a retrospective analysis using hierarchical models, while accounting for errors associated with the observation process (Kéry *et al.*, 2013). I illustrate the importance of fine-scale temporal dynamics of extrinsic conditions representing potential stressors for understanding contemporary species range shifts of two congeneric species, the Golden-winged Warbler (*Vermivora chrysoptera*) and Blue-winged Warbler (*Vermivora cynoptera*). The Golden-winged Warbler is a species of global conservation concern (Near Threatened, IUCN) and is undergoing precipitous declines (Sauer *et al.*, 2014). Capitalizing on the combination of a relatively comprehensive time-series data of species occurrences through use of North American Breeding Bird Survey data (USGS Patuxent Wildlife Research Center, 2012) and historical sequences of remotely sensed data (Pettorelli *et al.*, 2005) enabled estimation of the relationship between spatially-explicit annual habitat and climate changes in relation to occupancy, extinction, and colonization probabilities over a 30-year period (1983-2012) at the range-wide scale. Specifically, I investigated the degree of support for the relative importance of three main drivers of species' range dynamics: temperature changes, habitat dynamics, and occupancy patterns in relation to congeneric species. I complement these analyses with tests of niche similarity to quantify the degree of niche overlap between species and to assess whether niche differentiation has occurred over time for each species. This study represents a powerful assessment of the consequences of fine-scale temporal variability of extrinsic stressors on population-level demographic processes that result in temporally variable range-wide dynamics.

3.3 Methods

3.3.1 Study system and breeding bird survey data

The Golden-winged Warbler is one of the fastest declining Nearctic-Neotropical warblers with an estimated -2.6% yearly rate of decline across its range (number of BBS routes,

n=439, (-3.57, -1.69, 2.5% and 97.5% credible intervals, CR)) between 1966 and 2012 (Sauer *et al.*, 2014). Regional differentiation in rates of change are evident with the USA populations declining at rate of -2.89% /year (*n* =376, (-3.85, -1.93, CR)) while Canadian populations are increasing by 0.55%/year (*n* =66, (-3.03, 4.08, CR)). The Blue-winged Warbler is the only other extant species within the *Vermivora* genera, and range-wide trends for this species indicate declines albeit at a much slower annual rate relative to the Golden-winged (*n*=761, -0.64 (-1.24, 0.09, CR) (Sauer *et al.*, 2014). The Golden-winged occupies a more north-western distribution often occurring at higher elevations, although the spatial pattern of occupancy appears to be dynamic and complex with blue-wings often replacing golden-wing populations after first contact (Shapiro *et al.*, 2004). Both species rely on shrublands and early successional forests characterized by heterogeneous conditions (Confer & Knapp, 1981). These disturbance dependent habitats have been declining over the range of both species due to reforestation and advancement of succession, suggesting a role for habitat limitation in range-wide population declines (Hunter *et al.*, 2001, Confer & Pascoe, 2003, Dettmers, 2003). Region-specific smaller scale assessments suggest that the Golden-winged Warbler is a habitat specialist relative to the broader vegetation conditions used by the Blue-winged Warbler (Confer & Knapp, 1981), however, niche breadth has not been examined for both species across their ranges nor with a focus on their temporal dynamics.

Additional factors thought to contribute to Golden-winged Warbler declines include contact with its sister species, especially hybridization, and climate change. Although the specific mechanisms regarding the role of contact and replacement by Blue-winged Warbler remain elusive, this may potentially arise due to negative consequences of interference interactions (Confer *et al.*, 2003), hybridization (Gill, 1997), conspecific attraction combined with priority effects following spring migration (Gotelli *et al.*, 2010), or a combination of demographic swamping by the generally more abundant Blue-winged Warbler and Allee effects (Etienne *et al.*, 2002, Vallender *et al.*, 2007). While recent historical climate change is associated with changing distributions, studies have been limited by a focus on northern range boundary shifts thus providing a spatially restricted glimpse into distributional changes (Hitch & Leberg, 2007). Despite the complexity of

factors potentially influencing both species, they represent three important axes of drivers of range dynamics: (1) habitat, (2) climate, and (3) presence of congeneric species. Previous work is limited by a focus on small-scale studies without an examination of the relative role of all three main factors driving both species' occupancy patterns and the underlying processes of extinction and colonization at the range-wide scale.

I used data collected by The North American Breeding Bird Survey (BBS) between 1982 and 2012. The BBS is a longitudinal Citizen Science monitoring program with coverage including southern Canada and the USA since 1968. Every year, volunteers record detection data across more than 5200 predefined routes. Point counts are performed every 0.8 km across the entire length of the route (39.4 km) with visual or auditory observations considered within a 0.4 km radius, resulting in a total of 50 equally spaced point counts. Censuses are performed during the breeding season and most routes are re-visited annually. For each species, I selected routes that covered its entire range over the 30-year period. Only records conforming to BBS weather standards were included in the occupancy models. There were a total of 331 routes for the Golden-winged Warbler and 632 routes for the Blue-winged Warbler, where each species had been detected at least once over the 30-year period. I used detection/non-detection data summarized over a composite of 10 stops, resulting in 5 spatial replicates for each route. Detection refers to a positive observation of a species, while non-detection refers to absence of the species. However, for the latter, non-detection may occur because the species is truly absent from the site, or the species may be present but not observed. Our measures of occupancy are thus interpreted at the scale of the route across the study region (Royle & Kery, 2007). Not all routes were surveyed over the 30-years, observers changed within and between routes, and routes were not run more than once a year.

3.3.2   Environmental covariates

I selected maximum temperature and the Normalized Difference Vegetation Index (NDVI) to describe variation in range-wide occupancy and related demographic parameters of extinction and colonization for both species. Maximum temperature is hypothesized to limit species distributions at broad spatial scales with extreme values

expected to directly influence thermoregulation or indirectly through trophic interactions (Cahill *et al.*, 2013) and has been applied in other studies (Root, 1988, Venier *et al.*, 1999). Extreme short-term maximum temperature is expected to represent conditions that individuals experience directly in each location compared to long-term averages that likely underestimate the importance of short-term variability. Furthermore, short-term climate (i.e. weather) and the use of maximum temperature as a proxy for an extreme climatic event can influence, localized species distributions, relative to mean conditions (Bateman *et al.*, 2012, Greenville *et al.*, 2012). Monthly average daily maximum temperatures (degrees Celsius) were derived from the gridded CRU 3.2.1 dataset (resolution of 50 km) and were averaged across the three primary breeding months of May, June and July for each year from 1982 to 2012 (Harris *et al.*, 2013).

NDVI is an index of productivity, and vegetation cover and greenness (Hernández-Clemente *et al.*, 2009). It is sensitive to changes in the amount of photosynthetic vegetation (Soudani *et al.*, 2012) and is thus able to detect inter-annual variation in horizontal vegetation structure especially notable in the earlier stages of succession (Martinuzzi *et al.*, 2012). I used NDVI as a measure of vegetation change to address the hypothesis that declines in productivity will positively influence extinction rates and negatively influence colonization. NDVI has been used previously in the context of understanding patterns in species' distributions (e.g., Andrew *et al.*, 2012) and may be linked to resource availability (Hurlbert, 2004). I derived seasonal measures of NDVI for each year between 1982 and 2012. NDVI is measured as the difference in reflectance between the near infrared and red bands divided by the sum of the two bands [(NIR – RED)/ (NIR + RED)]. The NDVI varies from -1 to 1, where negative values indicate an absence of vegetation (Myneni *et al.*, 1995, Tucker *et al.*, 2005). Data were obtained from the Global Inventory Modeling and Mapping Studies Satellite (GIMMS) data set that used the Advanced Very High Resolution Radiometer (AVHRR) instrument on the National Oceanic and Atmospheric Administration satellites (Tucker *et al.*, 2005) at a resolution of 8 km. I developed time series of NDVI values averaged across each bimonthly period covering the months of May through July for each year between 1982 and 2012, inclusive.

I spatially averaged covariate values across grid cells where a given BBS route was located. BBS routes across Canada (Environment Canada, 2012) and the USA (USGS Patuxent Wildlife Research Center, 2012) were combined into one spatial layer representing routes and any changes in location between the years 1982 and 2012, inclusive. Each covariate was standardized to a mean of 0 and a standard deviation of 1 across all years to facilitate interpretation and convergence. None of the continuous covariates were correlated $|r| > 0.45$ (Pearson correlation coefficient). All spatial data were projected using the equal area Behrmann projection.

3.3.3   Dynamic occupancy models

I modeled inter-annual variation in occupancy for each species separately at the range-wide scale between the years 1983 to 2012 applying the maximum likelihood based model of MacKenzie *et al.* (2003). This hierarchical model explicitly accounts for imperfect detection of a species, thus accounting for errors resulting from the observation process. Not accounting for detection probability may result in biased parameter estimates potentially influencing inference regarding the role of alternative covariates on species occupancy. Furthermore, occupancy may be under-estimated leading to incorrect statements regarding species extinction risks (Royle & Dorazio, 2008, Lahoz-Monfort *et al.*, 2014). Two assumptions of this hierarchical model include (1) the absence of false detections and (2) the assumption of closure within the sampling period (i.e. occupancy does not change). For the latter assumption, I consider the breeding season as the sampling period, which conforms both to the time when the data are collected by BBS surveyors and when the Golden-winged and Blue-winged Warbler are found in this region as they are Nearctic-Neotropical migratory species.

The dynamic (i.e. multi-year) occupancy model is a two-state first-order Markov chain. The model consists of two sub-models: (1) the ecological (i.e. state) process model and (2) the observation or detection model, which is dependent on the results of the ecological model, and describes the probability of detecting a species given that the site is occupied and thereby accounts for false negative errors (Type II error, or, error of omission). The ecological model is a function of the probabilities of colonization (γ) and

extinction (ε) and is conditional on the occupancy status in the previous time step (*t*). Specifically, the probability that a site is occupied in *t+1* is a function of two probabilities: (1) the probability that the site was unoccupied at time *t* and was colonized between time *t* and *t+1*, plus (2) the probability that the site was occupied in *t* and did not go extinct in *t+1* such as,

$$\psi_{t+1} = \psi_t \times (1 - \varepsilon_t) + (1 - \psi_t) \times \gamma_t.$$

This is also the equation for recursively calculating the derived probability of occupancy at time *t+1*. The linking of inter-annual dynamics accounts for temporal autocorrelation present in time-series data, whereby demographic estimates are not assumed to be independent (Royle & Dorazio, 2008).

Hierarchical dynamic site-occupancy models consist of two nested binomial generalized linear models. The first model describes the true state of occurrence (present *vs* absent) of a species. The true state of occurrence of the study species at each site, z_i, is binary and is modelled as a Bernoulli distributed random variable and represents the latent occurrence at a site,

$z_i \sim$ Bernoulli(ψ_i),

where ψ_i is occupancy probability of the species at site *i*. To account for the observation process, the second logistic regression describes detection and non-detection conditional on the presence of the species. This model reflects the observed data, $y_{i,j}$, for species at site *i* during the *j*th survey and is also distributed as a Bernoulli random variable with success rate the product of z_i (true distribution) and detection probability $p_{i,j}$ such as,

$y_{ij}|z_i \sim$ Bernoulli$\left(z_i \times p_{ij}\right)$.

I incorporated site-specific covariates to model the first year probability of occupancy (ψ_1), extinction (ε), colonization (γ), and detection probabilities (*p*). First-year occupancy was modeled as function of the site-level covariates of maximum temperature and NDVI. Variation in detection probability was modelled as a function of a site-level

covariate, the date of the survey, due to the design of BBS surveys where routes are typically surveyed only once in a season, necessitating the use of spatial replicates. I ascribed the Julian date (hereafter DATE) representing the date each survey was run within a year, where numbering started on January 1st. I expected route surveys run later in the breeding season would result in lower detections.

To assess the role of changes in climate relative to habitat dynamics, annual colonization and extinction probabilities were modelled as a function of maximum temperature (TMAX) and NDVI, for each site i and for each year t preceding the detection data. Because time lags may occur between species' responsiveness to changing extrinsic conditions (Devictor *et al.*, 2012, van de Pol *et al.*, 2013), to capture the importance of annual temporal dynamics in climate and habitat, these covariates were specified for each site for each year, using a 1-year lag period (e.g., Gardner *et al.*, 2014). Additionally, the naïve detection (i.e. not accounting for detection errors) for each species was included as a covariate for each of the opposing species (SP). I hypothesized that the presence of the alternate species as a covariate would negatively influence probability of extinction and positively influence colonization probability.

3.3.4   Model selection, goodness of fit, and derived parameters

To test for time-dependence effects in extinction, colonization, and detection parameters, I formulated the model using a means parameterization, such that an intercept α represents the mean estimate in each year k across i sites. I compared time-dependent global models to models assuming constants rates over time. The most complex logistic model with covariate effects described first-year probability of occupancy across i sites as,

$$\text{logit}(\psi_{i,1}) = \alpha_0 + \beta_1 \times \text{TMAX}_{i,k} + \beta_2 \times \text{TMAX}^2_{i,k} + \beta_3 \times \text{NDVI}_{i,k} + \beta_4 \times \text{NDVI}^2_{i,k} + \beta_5 \times \text{TMAX}_{i,k} \times \text{NDVI}_{i,k} \, ,$$

while colonization (γ), extinction (ε), and detection (p) were modeled using a means parameterization of year k across i sites,

$$\text{logit}(\gamma_{i,k}) = \alpha_{i,k} \times \text{year}_i + \beta_1 \times \text{TMAX}_{i,k} + \beta_2 \times \text{TMAX}^2_{i,k} + \beta_3 \times \text{NDVI}_{i,k} + \beta_4 \times \text{NDVI}^2_{i,k} + \beta_5 \times \text{TMAX}_{i,k} \times \text{NDVI}_{i,k} + \beta_6 \times \text{SP}_{i,k} ,$$

$$\text{logit}(\varepsilon_{i,k}) = \alpha_{i,k} \times \text{year}_i + \beta_1 \times \text{TMAX}_{i,k} + \beta_2 \times \text{TMAX}^2_{i,k} + \beta_3 \times \text{NDVI}_{i,k} + \beta_4 \times \text{NDVI}^2_{i,k} + \beta_5 \times \text{TMAX}_{i,k} \times \text{NDVI}_{i,k} + \beta_6 \times \text{SP}_{i,k},$$

$$\text{logit}(p_{i,k}) = \alpha_{i,k} \times \text{year}_i + \beta_1 \times \text{DATE}_{i,k}.$$

Based on initial comparisons, time-constant models in colonization, extinction, and detection parameters were not highly supportive, and thus I continued to evaluate all time-dependent model sets using a hierarchical approach (Kéry *et al.*, 2010, Sadoti *et al.*, 2013). I developed a global model and evaluated model subsets using backward variable selection in three stages corresponding to the three parameters with >1 covariate: first-year occupancy, colonization, and extinction. Keeping all variables constant for colonization and extinction probability, I sequentially removed variables from first-year occupancy. I adhered to certain constraints, such as the retention of linear effects when higher order quadratic or interactions were included in the model. I selected the model with the lowest AIC (or within 2 AIC values) and performed the second stage of model selection on colonization based on the previously described procedure. Stage three focused on model selection for extinction probability.

Models were evaluated using information-theoretic model selection methods using AIC, which is defined as $-2\text{logL}(\theta\|y) + 2K$, where $\text{logL}(\theta\|y)$ is the maximized log-likelihood of the model parameters given the data and K is the number of estimable parameters (Burnham, 2002). I discarded models that did not converge (only two, Blue-winged Warbler: time constant, and model with time on detection). All competitive

models were inspected to ensure that none contained non-informative parameters if falling within 2 AIC of the top supported model (Arnold, 2010). Model sets for each species resulted in models with relatively equal support based on the <2 AIC criteria, for which I subsequently applied model-averaging techniques.

To describe uncertainty in the derived parameter, annual probability of occupancy in all but the first year, I applied a nonparameteric bootstrapping using 1000 replicates. Goodness of fit of the top model was assessed using a parameteric bootstrapping procedure, with 1000 replications, and is based on the chi-square test statistic (Kéry *et al.*, 2010). I measured turnover (*tau*) to provide an estimate of annual variation in the rate of reestablishment of a previously occupied site, (i.e. $Pr(z[i, t-1] = 0 \mid z[i, t] = 1)$, where

$$tau = \gamma_{t-1} \times (1 - \Psi_{t-1}) / (\gamma_{t-1} \times (1 - \Psi_{t-1}) + \Phi_{t-1} \times \Psi_{t-1}),$$

(Royle & Dorazio, 2008). Turnover estimates were based on 1000 parameteric bootstrapped simulations.

All analyses were performed with R, version 2.15.3 (R Core Team, 2013). Species co-occurrence metrics and null model runs were performed using the package '*bipartite*' (Dormann *et al.*, 2008a) and '*vegan*' (Oksanen *et al.*, 2013), and the hierarchical dynamic occupancy models were run using the package '*unmarked*' (Fiske & Chandler, 2011).

3.3.5   Quantifying patterns of species co-occurrence

To measure temporal patterns in spatial segregation I used the C-score, which quantifies the degree of occurrence between species, leading to checkerboard patterns of species occurrences (Stone & Roberts, 1992). The C-score is calculated as $(R_i - S) \times (R_j - S)$ where S is the number of shared occurrences between species i and j. R_i and R_j represent the total number of occurrences of species i and j. Higher index values indicate less overlap and more segregation between pairs of species, while lower values indicate more aggregation in species co-occurrences. The togetherness metric was calculated to quantify the degree that the two species have identical patterns of occurrences, while jointly avoiding a site (Stone & Roberts, 1992). I calculated both metrics for the two focal

species, for each year between 1983 and 2012, inclusive, to evaluate the temporal variability in co-occurrence patterns. Metrics were normalized to scale between 0 and 1 to enable comparisons between years. I expected to find increasing levels of segregation over time based on previous work suggesting a role for competition between the two focal species (Confer *et al.*, 2003).

Given that the C-score is sensitive to the total number of occupied sites and number of shared occurrences, yearly C-scores were tested against a fixed-fixed null model. This form of null model preserves both row (sites, i.e. breeding bird survey routes) and column (species) totals with each simulation, such that the frequencies of occurrences are the same as the original data (Gotelli & Ellison, 2002). Random matrices were simulated by swapping random sub-matrices of the original site by species matrix. This method of null model construction, in combination with C-score quantification, has good statistical properties that reduces the chance of Type I and Type II errors and has sufficient power to detect deviation from non-random patterns (Gotelli, 2000, Gotelli & Ulrich, 2011). Null model runs were performed using 1000 burn-in iterations to remove the influence of transient effects, a thinning rate of 10, and a final construction of 100,000 random matrices. If the observed distribution is significantly larger than a null distribution, there is increased spatial segregation (less overlap in species occurrences) than expected by chance. Conversely, if the observed distribution is significantly smaller than the null distribution, there is higher spatial aggregation than expected by chance. Similar methods and null model specifications are commonly employed (Ulrich *et al.*, 2012, Heino, 2013, Larsen & Ormerod, 2014).

3.3.6   Measures of niche overlap

I measured niche overlap and divergence to address whether there is evidence for temporal changes in niche properties for each species over the 30-year period, and whether niches differ between species. For each species I measured niche overlap between the first (1983-1987, hereafter time 1) and last five-years (1998-2012, hereafter time 2) of the 30-year period. I spatially averaged environmental covariates for each of time 1 and 2, and summarized species occurrences by considering any BBS route where

the species was recorded at least once as a 'presence'. Interspecific niche overlap consisted of comparisons between species within the same time period. Niche overlap was measured in multivariate environmental space using Principal Components Analysis (PCA) after Broennimann *et al.* (2012) using Schoener's *D*-statistic that varies between 0 and 1, representing no and complete overlap, respectively. A kernel density function was applied to each species and time period to smooth density of occurrences in environmental space, a procedure addresses the problem of biases introduced due to variation in sampling effort and available habitat (Broennimann *et al.*, 2012). I applied two permutation tests to evaluate statistically the condition of niche equivalency and niche similarity (Warren *et al.*, 2008). Niche equivalency tests the null hypothesis that niches are identical whereby the empirical overlap between two time periods (or two species within a time period, see below) is compared to a distribution of simulated measures of overlap. The latter is calculated based on a random sample of pooled occurrences between the two periods, whereby the number of occurrences for each period is preserved. Secondly, I applied tests of niche similarity to test the hypothesis that observed niche overlap is not different from overlap measured based on observed niche in one time and random assignment of niche space in the second time period. If measures of overlap are greater than 95% of simulated values, niches are more similar than expected by chance, based on environmental conditions available in both periods.

Tests of niche similarity require delimiting an environmental background for sampling, and results may be sensitive to this parameterization (Warren *et al.*, 2008, Broennimann *et al.*, 2012). I evaluated the sensitivity of this result by applying two backgrounds: (1) using a biogeographic method to characterize habitat availability and selecting ecoregions where the species was detected, and (2) by selecting regions within a 50 km radius of each location. I selected 50 km as representing a plausible rate of movement and expansion over the 5-year time periods of comparisons based on empirical estimates of range expansion across a diversity of avian species (Chen *et al.*, 2011b). The results were not sensitive to this variation and results are based on the 50 km radius outcomes. Permutation tests were run with 1000 replicates using R v. 15.3 based on code in (Broennimann *et al.*, 2012).

3.4 Results

3.4.1 Temporal variation in occupancy dynamics

Based on model selection results for both species, there was strong evidence for time-dependent models of extinction, colonization, and detection probabilities (Table 3.9.1, 3.9.2), illustrating the non-stationarity in yearly parameter estimates. However, the parameterization of the most supported models differed between species. Given the data, six models for the Golden-winged Warbler had high levels of support with ΔAIC values <2. Based on the hierarchical model selection methods employed, the highest ranked models differed based on the covariates included on the extinction term. All six models included linear effects for temperature and NDVI, and the occurrence of the Blue-winged Warbler on the extinction term. They differed in their combinations of quadratic and interaction effects of the two environmental covariates. I was unable to derive model averaged parameter estimates across the six models due to the use of the difference model. Thus I subsequently focus on the highest ranked model in terms of AIC. Goodness-of-fit tests based on parametric bootstrap simulations (n= 1000) revealed no evidence for lack of fit for the Golden-winged Warbler ($p = 0.33$).

General trends in expected occupancy when adjusted to account for inter-annual variability in detection probabilities indicated a declining trend in occupancy from 1983 to 2012 (Fig. 3.8.1). Expected occupancy was approximately 1.5 times lower in the latter 15 years of the study period relative to the first (mean$_{1983-1997}$ ± SD = 0.463 ± 0.063, mean$_{1998-2012}$ = 0.304 ± 0.0454; Fig. 3.8.2). The importance of accounting for detection estimates (mean$_{1983-1997}$ = 0.199 ± 0.0385, mean$_{1998-2012}$ = 0.218 ± 0.050) was evident based on uncorrected naïve occupancy estimates (mean$_{1983-1997}$ ± SD = 0.296 ± 0.0417, mean$_{1998-2012}$ = 0.199 ± 0.0385). Despite variability in annual colonization estimates, probabilities were very low, and declined between the first 15 years and last 14 years (extinctions and colonizations are estimated for the following year, resulting in *n-1* years) (mean$_{1983-1997}$ ± SD = 0.157 ± 0.097, mean$_{1998-2011}$ = 0.073 ± 0.045). Extinction rates in the absence of the Blue-winged exhibited large inter-annual variation and were on average higher relative to colonization estimates (mean$_{1983-1997}$ ± SD = 0.152 ± 0.120,

$mean_{1998\text{-}2012} = 0.171 \pm 0.109$). Detection probability varied inter-annually and as expected, inversely as a function of Julian date within a year.

Factors influencing distribution of the Golden-winged Warbler differed depending on the parameter under consideration, where the size of the coefficients adjusted by their standard errors of the different covariates reflects the relative magnitude of effects (Cross & Beissinger, 2001). First-year occupancy of the Golden-winged Warbler model was influenced by maximum temperature and NDVI, and their interaction; however none of these estimates were significant (Table 3.7.1; Fig. 3.8.3). Similarly, despite significant effects of time across most years, parameter estimates for temperature and NDVI had negligible effects on colonization probabilities. These estimates were uninformative; based on non-significance and large 95% confidence intervals overlapping 0, however, they were included in the final model as they contributed to large net reductions in AIC. Based on the best supported model, extinction probabilities were influenced by maximum temperature and NDVI, but in opposite directions. Both linear covariate terms were significant with extinction positively related with maximum temperature and negatively associated with NDVI. The inclusion of naïve detections of the Blue-winged Warbler on the extinction probability term resulted in significantly larger extinction estimates when it was detected at a site (Fig. 3.8.4).

Based on information theoretic methods, only one model had a high level of support for the Blue-winged Warbler (Table 3.7.2). There was no evidence of lack of fit based on 1000 parametric bootstrap runs ($p = 0.67$). My retrospective analysis of Blue-winged Warbler occupancy patterns revealed inter-annual variability in predicted occupancy adjusted to account for detection probability, however, in contrast to the Golden-winged, changes in occupancy between the first and last 15 years were minimal ($mean_{1983\text{-}1997} = 0.461 \pm 0.0343$, $mean_{1998\text{-}2012} = 0.465 \pm 0.0353$; Fig. 3.8.2). Accounting for detection estimates ($mean_{1983\text{-}1997} = 0.294 \pm 0.0345$ $mean_{1998\text{-}2012} = 0.208 \pm 0.0273$) resulted in substantive differences from naïve occupancy estimates ($mean_{1983\text{-}1997} = 0.361 \pm 0.0434$ SD, $mean_{1998\text{-}2012} = 0.318 \pm 0.0349$) (Figs. 3.8.2, 3.8.5). There was an effect of time on detection probability which was influenced within a year by date of survey with

the average probability declining later in the breeding season. Colonization probabilities were relatively constant over time and small (mean$_{1983-1997}$ = 0.134 ± 0.034, mean$_{1998-2011}$ = 0.128 ± 0.032), and extinction probabilities increased slightly between the first 15 years and latter 14 years (mean$_{1983-1997}$ = 0.122 ± 0.039, mean$_{1998-2012}$ = 0.151 ± 0.070).

In contrast to the Golden-winged Warbler, the Blue-winged Warbler model depicted more complex relationships between each response and the covariates. Covariates describing occupancy probability were significant and estimates were highest at intermediate levels of NDVI and maximum temperature (Table 3.7.2, Fig. 3.8.3). Colonization varied annually and was highest at low maximum temperatures and low NDVI, however the significant interaction effect between the two covariates suggested higher probabilities were also associated with high temperatures and high NDVI, although the relationship was weaker. Extinction probabilities were lowest at high NDVI (>8000) within an intermediate temperature range, and also lowest at low levels of NDVI and a broader range of temperatures. There was a significant positive association with Golden-winged Warbler detections and extinction probability, although based on standardized regression coefficients this covariate was ranked 4th out of 6 (where 1 is highest magnitude) due to large standard errors (Figs. 3.8.3, 3.8.6).

Turnover rates for both species exhibited inter-annual variability (Fig. 3.8.7). Annual rates ranged between average estimates of 0.00000349 and 0.6695 (mean ± SD, 0.1877 ± 0.1575, n=1000 bootstrapped samples) and 0.0869 and 0.308 (mean ± SD, 0.166 ± 0.0555) for the Golden-winged and Blue-winged Warblers, respectively.

3.4.2   Patterns of species occurrences

A comparison of naïve occupancy estimates (i.e. not accounting for detection probability) illustrates two striking patterns, (1) range-wide estimates of naïve occupancy between the two species begins to diverge in the mid-1990s, with the Golden-winged exhibiting larger apparent decline, and (2) proportional representation of the Blue-winged within the Golden-winged Warbler range has increased slightly over time and since 2005 has achieved occupancy levels similar to the Golden-winged (Fig. 3.8.8).

Despite similar naïve occupancy estimates across the two species within the Golden-winged Warbler range, C-score estimates suggest a high degree of spatial segregation in the actualized pattern of occupancy (Fig. 3.8.9). Over time, the C-score generally increased from 0.7930 ± 0.0455 (mean $\pm$ SD over first five years) to 0.8913 ± 0.0422 (mean $\pm$ SD over last five years), indicating increased spatial segregation over time. C-score metrics were significant for most years based on null model randomization tests ($p < 0.05$). The togetherness score were overall low and decreased on average from the first five to last five years (0.106 ± 0.0254 to 0.0625 ± 0.0239), suggesting a decline in the number of joint occurrences on surveyed BBS routes, with two-third of all years resulting in significance based on null on model tests ($p < 0.05$).

3.4.3   Tests of niche equivalency and similarity

Across both intraspecific temporal niche comparisons and interspecific niche comparisons, the observed measures of niche overlap based on Schoener's *D*-statistic fell below the 95% confidence intervals based on tests of niche equivalency, suggesting that niches between all species and time period combinations were not identical (Table 3.7.3). Niche overlap index values were highest for temporal niche comparisons of Golden-winged Warblers and lowest for temporal niche comparisons of the Blue-winged. Interspecific niche overlap indices (i.e. between congenerics) was higher in both periods (1983-1987 and 1998-2012) than temporal niche overlap of the Blue-winged Warblers. Tests of niche similarity revealed that in all but one case, niche overlap was more similar than expected by chance from the environmental conditions available, based on higher overlap values than the null distributions. Randomization tests were not significant for Blue-winged Warblers when comparing time 1 to random selection of time 2 distributions, but were significantly similar in the other direction. Golden-winged Warbler niche breadth was narrower across both maximum temperature and NDVI axes, was detected at sites that were on average 2°C cooler and regardless of 5-year period occurred within a subset of NDVI conditions relative to its congeneric (Table 3.7.4; Figs. 3.8.10 - 3.8.12). The Blue-winged Warbler was detected across a much wider spread of habitat conditions based on NDVI values, which were on average slightly higher than the Golden-winged Warbler.

3.5 Discussion

In an era characterized by increasing rates and extents of environmental change, an understanding of factors influencing species range dynamics has never been more salient. The predominance of correlative approaches for approximating expected future species' distributions relies heavily on the assumption of species equilibrium, with environmental covariates typically summarizing long-term averages. Notwithstanding the biological significance of long-term averages, few studies explore fine-scale temporal variability in environmental conditions on species range dynamics at large spatial extents. I have shown that inter-annual variation in weather and habitat successional dynamics are associated with species range dynamics of two congeneric species. By relating short-term extrinsic environmental conditions to changes in local extinction rates, my results enable us to understand their relevance as drivers of the demographic processes that underlie range dynamics. The strength of our hierarchical modeling approach includes integration of time-dependent covariates thought to contribute to changes in population-level processes while simultaneously accounting for spatial and temporal variation in detection probabilities.

Methods that enable inference between demographic processes that drive species distributions and multiple competing hypotheses regarding species declines are important for understanding the consequences of environmental change on broad-scale range dynamics. Notably, I have demonstrated the importance of considering fine temporal scale variation of extrinsic environmental changes on occupancy dynamics. While much research has focused on understanding the consequences of long-term average climate change on species range-wide distributions, my results emphasize the important contributions of short-term changes in extreme temperature on time-dependent occupancy probabilities. Temporal variations in weather have shown to be important for explaining broad-scale distributions over shorter time scales (Reside *et al.*, 2010, Bateman *et al.*, 2012, Greenville *et al.*, 2012), which highlights the relevance of variables that describe localized conditions in time. Variables that capture weather and extreme events that characterize the conditions individuals are exposed to in the short-term are of particular importance when these coincide with critical sensitive life history stages, for example by

lowering reproductive success (Langin *et al.*, 2009, Albright *et al.*, 2011, Levine *et al.*, 2011). My work in particular, provides evidence for an association between short-term climate extremes and the probability that sites become locally extinct. With the magnitude and frequency of extreme weather events expected to increase (IPCC, 2012), my findings underscore the importance of addressing the effects of finer temporal-scale variation in extreme climate events on species persistence alongside the role of long-term climate means on species' distributional shifts.

The variability and apparent idiosyncrasy in observed changes in species distributions over time and space has focused attention towards consideration of biotic interactions and direct measures of habitat change in addition to abiotic factors (Van der Putten *et al.*, 2010, Mair *et al.*, 2012, González-Salazar *et al.*, 2013, Wisz *et al.*, 2013). In the context of both improving understanding of species responses to multiple stressors and development of sound management practices, a focus on the relative importance of multiple factors is required. Based on the temporal scale of analysis, factors associated with increased extinction risk were species-specific but biotic factors consistently contributed to larger magnitude of effects relative to abiotic (maximum temperature) elements. The highest ranking covariate associated with Golden-winged Warbler extinction probabilities was the occurrence of its congeneric species at a site, providing additional support for the long-held view that Blue-winged Warblers replace Golden-winged Warblers (Gill, 1997, Gill, 2004). Regardless of the significance of this association, it remains challenging to elucidate specific mechanisms by which this occurs. Despite local-scale evidence for interference competition of the dominant Blue-winged Warbler (Confer *et al.*, 2003), patterns of sympatry suggest that the strength of such interactions is insufficient on its own to contribute to replacement patterns between the species (Confer, 2006). Other postulated non-mutually exclusive mechanisms that require further testing include the potential for priority effects following spring migration, resource exploitation of available habitats by the typically more relatively abundant Blue-winged Warbler, and Allee effects associated with small populations. Finally, temporal variation in occupancy may result from limiting factors occurring during the migration period and throughout the nonbreeding season (Wilson *et al.*, 2011). Nonetheless, I have

addressed both known (habitat loss, presence of congeneric for the Golden-winged Warbler) and hypothesized (climate change) threatening processes associated with the breeding season (Buehler *et al.*, 2007). This advances our understanding of drivers of temporal variation of range dynamics for these two species, and provides support for the integration of finer-scale temporal dynamics of threatening processes.

Despite the reliance of higher trophic level consumer species on habitat features (i.e. vegetation structure and composition), there still remains a relatively poor understanding of their potentially interacting effects on range-wide species' distributions (Warren *et al.*, 2001, Sarmento Cabral *et al.*, 2013). My results show that changes in habitat, using NDVI as a proxy, were strongly associated with extinction risk at broad scales. Further, when accounting for standard errors of covariate parameter estimates, NDVI was consistently ranked higher with respect to magnitude of effect on expected extinction probabilities for both species relative to extreme temperature. This strong signal of inter-annual habitat dynamics on estimated extinction probabilities suggests that species are responding to proximate changes in habitat at fine temporal scales. Indeed, broad-scale land-use changes leading to loss of early successional habitats due to afforestation have been implicated in regional declines in Golden-winged Warbler populations (Litvaitis, 1993). In addition to the narrow habitat breadth of Golden-winged Warblers, these early successional habitats are likely to occur in this stage for relatively short periods of time, which combined with regional patterns of afforestation amplify these habitats as limiting factors. Despite the relatively few studies that consider both habitat and climate changes on species' distributions (Clavero *et al.*, 2011), these findings emphasize the need to consider short-term dynamics of habitat changes, which may arise due to natural processes such as succession or anthropogenic causes resulting in land-use land-cover change.

The relative importance of extrinsic factors on species' range dynamics are likely to vary as a function of the temporal and spatial scale under consideration. In this work, I focused on the importance of habitat and climate variation at a single temporal scale (annual), and thus the results do not preclude the relevance of longer-term climate change

averages on species' distributions. My selection of covariates and time-frames was driven by the expectation that birds possess life-history strategies that increase individual responsiveness to short-term changes in extreme climate events or habitat conditions (Parmesan, 2001).While most distribution models address the role of abiotic factors fixed on coarse temporal scales (i.e. >5 years), fine temporal scales are more likely to match the scale at which populations respond, and informs us of conditions faced by individuals (Guisan & Thuiller, 2005, van de Pol *et al.*, 2013). While time-lags in species' responsiveness to climate changes have been suggested (Menéndez *et al.*, 2006, Devictor *et al.*, 2012, La Sorte & Jetz, 2012), these studies have applied different approaches that included assessments using only portions of species' ranges, emphasized changes in range boundaries, and generally applied long-term climate means. Further work examining the role of the scale of time-lagged responses could provide information relevant for population dynamics and development of ecologically fine-tuned predictive models under climate change. Despite, this previous studies have applied similar scales of temporally lagged data for similar species (e.g., Wilson *et al.*, 2011, Price *et al.*, 2013, Gardner *et al.*, 2014). Consideration of finer spatial scale information such as percent forest cover or microclimate (Streby *et al.*, 2012, Potter *et al.*, 2013) or other indices of extreme climate such as magnitudes of drought or heat waves (e.g., Albright *et al.*, 2010), provide directions for further inquiry. By conducting this analysis at the range-wide scale and focusing on estimation of the underlying processes of extinction and colonization that drive range dynamics, I overcome some of the limitations of other approaches and provide more complete picture of broad-scale pattern and processes.

By applying multiple approaches to understand species range dynamics, I provide a more comprehensive picture of the temporal and spatial range dynamics as they relate to multiple niche axes. The range-wide characterization of niche breadth is consistent with more localised accounts that the Golden-winged Warbler is considered a habitat specialist relative to its congeneric (Confer & Knapp, 1981), tending to occur in a narrow range of habitat conditions (NDVI) which are generally a subset of the Blue-winged Warbler's broader habitat preferences. Tests of niche similarity between both species imply that observed niche differentiation is a function of habitat preferences and not due

to temperature and NDVI differences between the available habitats. Niche differentiation between the two congeneric species occurs primarily along the maximum temperature gradient with the Golden-winged occupying cooler regions on average and the Blue-winged occurring across a broader range of thermal conditions. Species with narrow niche breadths are often more vulnerable to extinction (Gaston & Fuller, 2009, Devictor *et al.*, 2010), which is reflected in the temporal trend in declining range-wide expected occupancy for the Golden-winged Warbler. In combination with the dynamic occupancy models, management for population recovery or retention in regions devoid of Blue-winged Warblers with a focus on maintaining or creation of habitat reflecting optimal conditions is a likely relevant approach.

Evidence for temporal niche conservatism suggests species' are responding to changing climates by moving into favourable conditions, and can be an important gauge of species' ability to buffer changing climatic conditions (Devictor *et al.*, 2012). These results suggest that both species are niche tracking based on contemporary temporal comparisons of niche breadth and tests of niche similarity for each species between 1983-1987 and 1998-2012. However, evidence of niche conservatism on its own does not provide information about range shifts *per se* nor population status. While both species have significantly similar contemporary niches than expected by chance, temporal trends in expected range-wide occupancy over the 30-year period were clearly divergent between the two species. Furthermore, the Golden-winged Warbler appears to be occupying cooler regions than it has in the past (Fig, 3.8.11). These cooler areas tend to occur along its expansion front, in areas that are largely devoid of the Blue-winged Warbler. Local extinction from warm-edge areas were in many cases within thermal niche breadth of the Golden-winged Warbler, but have been colonized by its congeneric. Whether these cooler regions truly represent marginal conditions often associated with range edges and potential sinks (Caughley *et al.*, 1988, Sexton *et al.*, 2009) and whether causal reasons for occupancy are related to expansion pressure from the Blue-winged Warbler requires further research. Local-scale studies targeting demographic variation across environmental gradients and varying levels of co-occurrence of its congeneric

would provide valuable insights into population responses and limitation associated with more marginal environmental conditions.

Dynamic occupancy models are a powerful modeling approach in part as it is possible to capture time-dependent variation in parameters as a function of dynamic variables hypothesized to influence range dynamics, thus providing the potential to inform management actions addressing declines. For both species, species-specific relationships between temperature, habitat, and congeneric occurrence were strongly related to extinction probabilities. However, covariate relationships were generally not detected in relation to colonization probabilities, except in the case of the Blue-winged Warbler where there was a statistically significant interaction effect between NDVI and temperature. There are a number of plausible reasons for this outcome. For both species, time-dependency in colonization estimates were important, however, for the Golden-winged in particular, colonization events were generally low in any given year precluding identification of significant covariates. Despite this, the directionality of covariate effects was in the expected direction (e.g., increasing temperature and NDVI associated with opposite trends). As colonization probability may be related to the presence of conspecifics, including a measure of spatial autocorrelation of occupancy may have revealed important associations (Melles *et al.*, 2011, Altwegg *et al.*, 2013, Bled *et al.*, 2013). It is possible explanatory variables were summarized at a scale too coarse to adequately capture the colonization process, while the use of population-level abundance data may have revealed important associations not possible by using binary presence-absence. Interestingly, in other dynamic models specified at large scales, relationships between colonization and explanatory variables generally remained marginal in their significance (e.g., Sadoti *et al.*, 2013).

I assumed associations between temperature extremes influenced range dynamics of focal avian species and but habitat temporal dynamics were independent of climate change influences. While vegetation may act as a proxy for climate, and cross-scale feedbacks between climate, vegetation, and wildlife are expected (Soranno *et al.*, 2014), I have presented a simplified analysis to illustrate the fundamental importance of time-

varying dynamics of climate and habitat on range dynamics, which are generally not considered. Given my focus on inter-annual variability in temperature and habitat, I believe this assumption is warranted due in part to the short temporal scale of analysis. In addition, previous work demonstrating a link between climate change, in particular precipitation, on inter-annual variability of NDVI suggests our use of NDVI captured vegetation response to climate change, despite not directly accounting for its effect (Krishnaswamy *et al.*, 2013, Zeng *et al.*, 2013). Although the influence of climatic extremes on plants remains largely understudied (Reyer *et al.*, 2013), the lag in response time of plant species to changing climate conditions is likely more pronounced given the intrinsic ability of birds to more quickly respond to changing extrinsic conditions (Kissling *et al.*, 2010).

Finally, I did not explicitly include hybrids of both focal species in the analysis. Both the Golden-winged and Blue-winged Warbler can produce viable hybrid offspring, which tend to exhibit distinct phenotypes. Hybridization with Blue-winged Warblers is considered a threat to declining pure Golden-winged Warbler types, in addition to loss of habitat due to forest maturation (Litvaitis, 1993, Gill, 1997, Vallender *et al.*, 2009a). However, recent studies demonstrate that genetic introgression is likely more symmetrical between the two species than previously thought, implying that hybridization may not favour one species over the other (Shapiro *et al.*, 2004, Dabrowski *et al.*, 2005, Vallender *et al.*, 2009b). If the pattern of hybridization is spatially homogenous then potential errors and biases associated with species misidentification (Miller *et al.*, 2011) due to cryptic hybridization (Vallender *et al.*, 2009a) may be minimized, or at least be equivalent across species.

Methods to understand the relative importance of multiple environmental factors on broad-scale species ranges generally use distribution modeling based on discrete time periods summarizing long-term climate averages, and few include habitat dynamics. Such static approaches have so far been challenged methodologically with limits in particular related to assumptions of species equilibrium. These results add to the body of knowledge on the importance of short-term dynamics in both climate and habitat factors as limiting agents on species range dynamics. Long-term longitudinal monitoring data contributes vastly to our understanding of population dynamics at broad scales, providing process-

based insights into the consequences of global changes. This retrospective analysis emphasizes the important associations between time-varying environmental conditions and wildlife responses, however, such understandings rely critically on data collected over the long-term, at both broad spatial extents and over fine-scale time periods (Magurran *et al.*, 2010). The use of remotely sensed NDVI as a habitat proxy suggests that fine-scale inter-annual variation in horizontal vegetation structure especially notable in the earlier stages of succession (Martinuzzi *et al.*, 2012) captured important variations in occupancy dynamics, and importantly differences between occupied habitats of the two species. I have shown here how both dynamic occupancy modelling and quantitative comparisons of measures of niche overlap provide complementary insights into temporal range dynamics. The application of modeling approach that accounts for imperfect detection revealed demographic non-stationarity in relation to time-varying covariates representing multiple factors hypothesized to influence species' distributional changes. This research adds to the body of evidence underscoring the importance of biotic factors as an integral component of models of species' distributions and their range dynamics, and the need to consider finer-temporal scale variation in dynamic threats.

3.6   Acknowledgements

3.7 Tables

Table 3.7.1 Parameter estimates for the top ranked dynamic occupancy model of the Golden-winged Warbler. *Psi*: first year occupancy, *gamma*: colonization, *eps*: extinction, and *p*: detection probabilities.

Model

psi~1 gamma~ (year - 1) + tmxs + ndvis + tmxs * ndvis eps~ (year - 1) + tmxs + ndvis + bwcov

p~ (year - 1) + jul

Initial:	Estimate	SE	z	P(>|z|)
	-0.103	0.216	-0.477	0.633
Colonization	**Estimate**	**SE**	**z**	**P(>|z|)**
year1983	-0.5924	0.4107	-1.442	1.49E-01
year1984	-1.698	0.6	-2.83	4.66E-03
year1985	-0.9908	0.5005	-1.98	4.77E-02
year1986	-1.6375	0.7067	-2.317	2.05E-02
year1987	-1.0728	1.2969	-0.827	4.08E-01
year1988	-4.6637	36.411	-0.128	8.98E-01
year1989	-2.2799	0.797	-2.861	4.23E-03
year1990	-2.7776	0.8019	-3.464	5.33E-04
year1991	-2.3796	0.6332	-3.758	1.71E-04
year1992	-1.1102	0.4051	-2.741	6.13E-03
year1993	-2.6235	0.8031	-3.267	1.09E-03
year1994	-1.7262	0.3866	-4.465	8.01E-06
year1995	-1.9728	0.3977	-4.961	7.02E-07
year1996	-1.5678	0.3283	-4.775	1.80E-06
year1997	-2.0574	0.4206	-4.892	1.00E-06
year1998	-2.602	0.4745	-5.484	4.16E-08
year1999	-1.7156	0.4027	-4.261	2.04E-05
year2000	-2.2348	0.7291	-3.065	2.18E-03
year2001	-3.6071	1.4374	-2.509	1.21E-02
year2002	-1.851	0.3616	-5.119	3.07E-07
year2003	-3.2838	0.8669	-3.788	1.52E-04
year2004	-2.3332	0.3872	-6.026	1.68E-09

	Estimate	SE	z	P(>|z|)
year2005	-2.9769	0.6327	-4.705	2.54E-06
year2006	-2.1314	0.3861	-5.521	3.38E-08
year2007	-3.5125	0.9269	-3.79	1.51E-04
year2008	-2.1492	0.3819	-5.628	1.82E-08
year2009	-3.3968	0.9003	-3.773	1.61E-04
year2010	-9.6056	13.1603	-0.73	4.65E-01
year2011	-2.5628	0.6048	-4.238	2.26E-05
Tmxs	-0.1452	0.0935	-1.553	1.20E-01
Ndvis	-0.0157	0.0782	-0.201	8.41E-01
tmxs:ndvis	-0.1334	0.0767	-1.738	8.22E-02
Extinction:	**Estimate**	**SE**	**z**	**P(>|z|)**
year1983	-2.1939	0.822	-2.67	7.63E-03
year1984	-0.0546	0.454	-0.12	9.04E-01
year1985	-1.8489	0.768	-2.41	1.60E-02
year1986	-1.4982	0.676	-2.22	2.66E-02
year1987	-1.862	0.562	-3.31	9.24E-04
year1988	-2.8232	0.814	-3.47	5.21E-04
year1989	-1.9919	0.487	-4.09	4.38E-05
year1990	-3.5754	1.313	-2.72	6.46E-03
year1991	-2.1369	0.563	-3.8	1.46E-04
year1992	-3.172	1.168	-2.72	6.61E-03
year1993	-0.7363	0.326	-2.26	2.39E-02
year1994	-1.7799	0.536	-3.32	9.05E-04
year1995	-1.4143	0.348	-4.06	4.83E-05
year1996	-2.0143	0.501	-4.02	5.75E-05
year1997	-0.8254	0.353	-2.34	1.93E-02
year1998	-0.6259	0.367	-1.71	8.82E-02
year1999	-2.4202	0.787	-3.07	2.11E-03
year2000	-2.6519	0.788	-3.36	7.69E-04
year2001	-0.7462	0.344	-2.17	3.02E-02
year2002	-2.1763	0.771	-2.82	4.75E-03
year2003	-0.6215	0.331	-1.88	6.08E-02
year2004	-2.8361	1.318	-2.15	3.14E-02

	Estimate	SE	z	P(>|z|)
year2005	-1.3176	0.452	-2.92	3.55E-03
year2006	-2.0996	0.581	-3.62	2.99E-04
year2007	-2.4364	0.9	-2.71	6.81E-03
year2008	-1.8703	0.605	-3.09	1.98E-03
year2009	-3.0425	1.887	-1.61	1.07E-01
year2010	-1.2057	0.567	-2.13	3.34E-02
year2011	-1.5424	1.4	-1.1	2.71E-01
Tmxs	0.2868	0.113	2.55	1.08E-02
Ndvis	-0.4055	0.101	-4	6.31E-05
bwcov1	1.3324	0.209	6.37	1.92E-10
Detection:	**Estimate**	**SE**	**z**	**P(>|z|)**
year1983	-1.095	0.1565	-7	2.61E-12
year1984	-1.413	0.1491	-9.47	2.74E-21
year1985	-1.365	0.2375	-5.75	9.06E-09
year1986	-1.683	0.1813	-9.28	1.64E-20
year1987	-1.612	0.1684	-9.57	1.05E-21
year1988	-1.755	0.3031	-5.79	7.08E-09
year1989	-1.383	0.1351	-10.23	1.43E-24
year1990	-1.534	0.1373	-11.17	5.78E-29
year1991	-1.675	0.1351	-12.4	2.59E-35
year1992	-1.34	0.1273	-10.53	6.30E-26
year1993	-1.629	0.1291	-12.62	1.72E-36
year1994	-1.203	0.1264	-9.51	1.85E-21
year1995	-1.332	0.129	-10.32	5.68E-25
year1996	-1	0.1223	-8.17	2.99E-16
year1997	-1.081	0.1257	-8.6	8.14E-18
year1998	-1.185	0.1382	-8.57	1.03E-17
year1999	-1.194	0.1652	-7.23	4.92E-13
year2000	-1.656	0.1692	-9.79	1.22E-22
year2001	-1.838	0.1788	-10.28	8.90E-25
year2002	-0.841	0.1514	-5.56	2.77E-08
year2003	-1.277	0.1468	-8.7	3.36E-18
year2004	-0.732	0.1617	-4.53	6.03E-06

year2005	-1.355	0.1766	-7.67	1.74E-14
year2006	-1.196	0.1589	-7.52	5.34E-14
year2007	-1.375	0.1469	-9.36	7.74E-21
year2008	-1.132	0.1525	-7.42	1.14E-13
year2009	-1.499	0.1651	-9.08	1.12E-19
year2010	-1.633	0.162	-10.08	7.08E-24
year2011	-1.164	0.1711	-6.8	1.01E-11
year2012	-1.416	0.2625	-5.39	6.92E-08
Jul	-0.331	0.0284	-11.66	2.08E-31

Table 3.7.2 Parameter estimates for the top ranked dynamic occupancy model for the Blue-winged Warbler. *Psi*: first year occupancy, *gamma*: colonization, *eps*: extinction, and *p*: detection probabilities.

Model
psi~t1+n1+I(n1^2)+I(t1^2)
gamma~(year-1)+tmxs+ndvis+tmxs*ndvis
eps~(year-1)+tmxs+ndvis+I(ndvis^2)+I(tmxs^2)+tmxs*ndvis+gwcov
p~(year-1)+jul

Initial:	Estimate	SE	z	P(>|z|)
(Intercept)	0.0575	0.1715	0.335	0.737341
t1	0.3069	0.1396	2.199	0.027895
n1	0.8446	0.2111	4.001	0.000063
I(n1^2)	0.2606	0.0802	3.252	0.001147
I(t1^2)	-0.4998	0.1331	-3.756	0.000173

Colonization:	Estimate	SE	z	P(>|z|)
year1983	-2.0626	0.3168	-6.51	7.45E-11
year1984	-2.1216	0.3098	-6.85	7.51E-12
year1985	-2.0199	0.2894	-6.98	2.96E-12
year1986	-1.7326	0.2867	-6.04	1.52E-09
year1987	-2.0877	0.3312	-6.3	2.91E-10
year1988	-1.3488	0.2293	-5.88	4.04E-09
year1989	-2.3441	0.4434	-5.29	1.25E-07
year1990	-2.2597	0.3435	-6.58	4.77E-11
year1991	-1.6478	0.2499	-6.59	4.28E-11
year1992	-2.0274	0.3097	-6.55	5.92E-11
year1993	-1.7742	0.2463	-7.2	5.93E-13
year1994	-1.8536	0.2567	-7.22	5.18E-13
year1995	-1.6314	0.2396	-6.81	9.77E-12

year1996	-1.5369	0.228	-6.74	1.57E-11
year1997	-1.899	0.2767	-6.86	6.75E-12
year1998	-1.7438	0.2727	-6.4	1.60E-10
year1999	-1.7018	0.3001	-5.67	1.43E-08
year2000	-2.3652	0.4707	-5.02	5.04E-07
year2001	-1.8361	0.288	-6.38	1.81E-10
year2002	-1.7293	0.274	-6.31	2.76E-10
year2003	-2.2021	0.3958	-5.56	2.64E-08
year2004	-1.366	0.2618	-5.22	1.81E-07
year2005	-2.2441	0.5188	-4.33	1.52E-05
year2006	-1.952	0.3719	-5.25	1.53E-07
year2007	-1.9771	0.3691	-5.36	8.46E-08
year2008	-1.8141	0.294	-6.17	6.80E-10
year2009	-2.4101	0.429	-5.62	1.93E-08
year2010	-1.7174	0.2898	-5.93	3.08E-09
year2011	-2.2309	0.4026	-5.54	2.99E-08
Tmxs	-0.0916	0.0439	-2.09	3.69E-02
Ndvis	0.0773	0.0563	1.37	1.70E-01
tmxs:ndvis	0.2007	0.0561	3.58	3.46E-04

Extinction:	Estimate	SE	z	P(>|z|)
year1983	-1.97405	0.3325	-5.936	2.92E-09
year1984	-1.42761	0.2983	-4.786	1.70E-06
year1985	-2.13288	0.4054	-5.261	1.44E-07
year1986	-2.59989	0.533	-4.878	1.07E-06
year1987	-1.55857	0.3145	-4.955	7.23E-07
year1988	-2.16057	0.3817	-5.66	1.51E-08
year1989	-2.24973	0.3391	-6.635	3.25E-11
year1990	-2.19315	0.3603	-6.086	1.15E-09
year1991	-2.33466	0.3828	-6.099	1.07E-09

year1992	-1.82226	0.322	-5.66	1.52E-08
year1993	-2.67039	0.4176	-6.394	1.62E-10
year1994	-1.71145	0.2884	-5.935	2.94E-09
year1995	-1.83367	0.2484	-7.382	1.56E-13
year1996	-1.60088	0.2427	-6.595	4.25E-11
year1997	-1.78194	0.2937	-6.068	1.29E-09
year1998	-2.19204	0.3966	-5.527	3.26E-08
year1999	-1.61546	0.4027	-4.012	6.03E-05
year2000	-2.28239	0.3617	-6.31	2.79E-10
year2001	-1.61084	0.3542	-4.548	5.42E-06
year2002	-1.20819	0.311	-3.885	1.02E-04
year2003	-2.13739	0.5301	-4.032	5.53E-05
year2004	-2.46198	0.4038	-6.097	1.08E-09
year2005	-2.02277	0.3341	-6.054	1.41E-09
year2006	-2.25289	0.4909	-4.589	4.45E-06
year2007	-1.17162	0.2536	-4.619	3.85E-06
year2008	-2.04125	0.4741	-4.306	1.66E-05
year2009	-1.33495	0.3112	-4.29	1.79E-05
year2010	-2.32583	0.705	-3.299	9.71E-04
year2011	-0.73267	0.4643	-1.578	1.15E-01
Tmxs	0.00868	0.0678	0.128	8.98E-01
Ndvis	-0.98073	0.0967	-10.145	3.48E-24
I(ndvis^2)	-0.23942	0.0314	-7.616	2.62E-14
I(tmxs^2)	0.37973	0.0466	8.148	3.69E-16
gwcov1	0.91967	0.216	4.257	2.07E-05
tmxs:ndvis	-0.16059	0.0667	-2.408	1.60E-02
Detection:	**Estimate**	**SE**	**z**	**P(>|z|)**
year1983	-0.666	0.0901	-7.39	1.48E-13
year1984	-0.635	0.0892	-7.12	1.09E-12
year1985	-0.973	0.1072	-9.08	1.13E-19

year1986	-0.879	0.0982	-8.96	3.37E-19
year1987	-1.121	0.0895	-12.52	5.69E-36
year1988	-0.878	0.0896	-9.8	1.15E-22
year1989	-0.949	0.0867	-10.94	7.42E-28
year1990	-0.933	0.0879	-10.61	2.63E-26
year1991	-1.069	0.0901	-11.86	1.99E-32
year1992	-0.909	0.0788	-11.53	9.74E-31
year1993	-1.038	0.0849	-12.22	2.53E-34
year1994	-0.881	0.0747	-11.8	3.95E-32
year1995	-0.78	0.0744	-10.48	1.08E-25
year1996	-0.613	0.0714	-8.58	9.17E-18
year1997	-0.635	0.0723	-8.78	1.60E-18
year1998	-0.997	0.0811	-12.3	8.78E-35
year1999	-1.322	0.0867	-15.24	1.80E-52
year2000	-1.276	0.0889	-14.36	9.88E-47
year2001	-1.358	0.0937	-14.49	1.41E-47
year2002	-1.184	0.0951	-12.45	1.42E-35
year2003	-1.167	0.0939	-12.43	1.79E-35
year2004	-1.434	0.104	-13.79	2.75E-43
year2005	-1.326	0.0849	-15.62	5.73E-55
year2006	-1.423	0.0923	-15.42	1.24E-53
year2007	-1.477	0.0945	-15.62	5.33E-55
year2008	-1.189	0.0905	-13.14	1.87E-39
year2009	-1.384	0.0934	-14.82	1.05E-49
year2010	-1.356	0.0961	-14.12	2.89E-45
year2011	-1.695	0.1068	-15.87	1.01E-56
year2012	-1.493	0.1219	-12.24	1.83E-34
Jul	-0.288	0.0142	-20.3	1.36E-91

Table 3.7.3 Temporal and interspecific measures of niche overlap (*D*-statistic) and tests of niche equivalency and similarity based on mean maximum temperature and NDVI. Time 1 refers to temporal niches summarized over BBS routes where each species was detected at least once between 1983 and 1987, and time 2 between 1998 and 2012, inclusive for the Golden-winged Warbler (GWWA) and Blue-winged Warbler (BWWA). Statistical test outcomes were not-significant (n.s., *P* > 0.05), or significantly similar (sig. sim., *P* < 0.01 (*)). Niche similarity tests were performed first by comparing the first element of the pairwise comparison (i.e. GWWA time 1) against a randomization the niche of the second element (i.e. GWWA time 2), and then vice versa.

Comparison	Niche overlap	Niche equivalency	Niche similarity
GWWA time 1 - GWWA time 2	0.497	sig. (*)	sig. sim. (*); sig. sim. (*)
BWWA time 1 - BWWA time 2	0.348	sig. (*)	n.s., sig. sim (*)
GWWA time 1 - BWWA time 1	0.374	sig. (*)	sig. sim. (*); sig. sim. (*)
GWWA time 2 - BWWA time 2	0.364	sig. (*)	sig. sim. (*); sig. sim. (*)

Table 3.7.4 Climate and habitat niche dimensions for golden- and Blue-winged Warblers. Maximum temperature and NDVI values were averaged over the breeding months of May, June, and July across North American Breeding Bird Survey routes where the species were detected between 1983-2012. Measures are means ± 1 SD.

	Golden-winged Warbler	Blue-winged Warbler
Mean seasonal maximum temperature	23.922 +/- 2.013	25.803 +/- 2.398
Mean seasonal NDVI	8299 +/- 625	8195 +/- 821
Mean latitudinal position	5019713 +/- 315055	4768016 +/- 270338
Mean longitudinal position	-8037606 +/- 659839	-7868999 +/- 605286

3.8   Figures
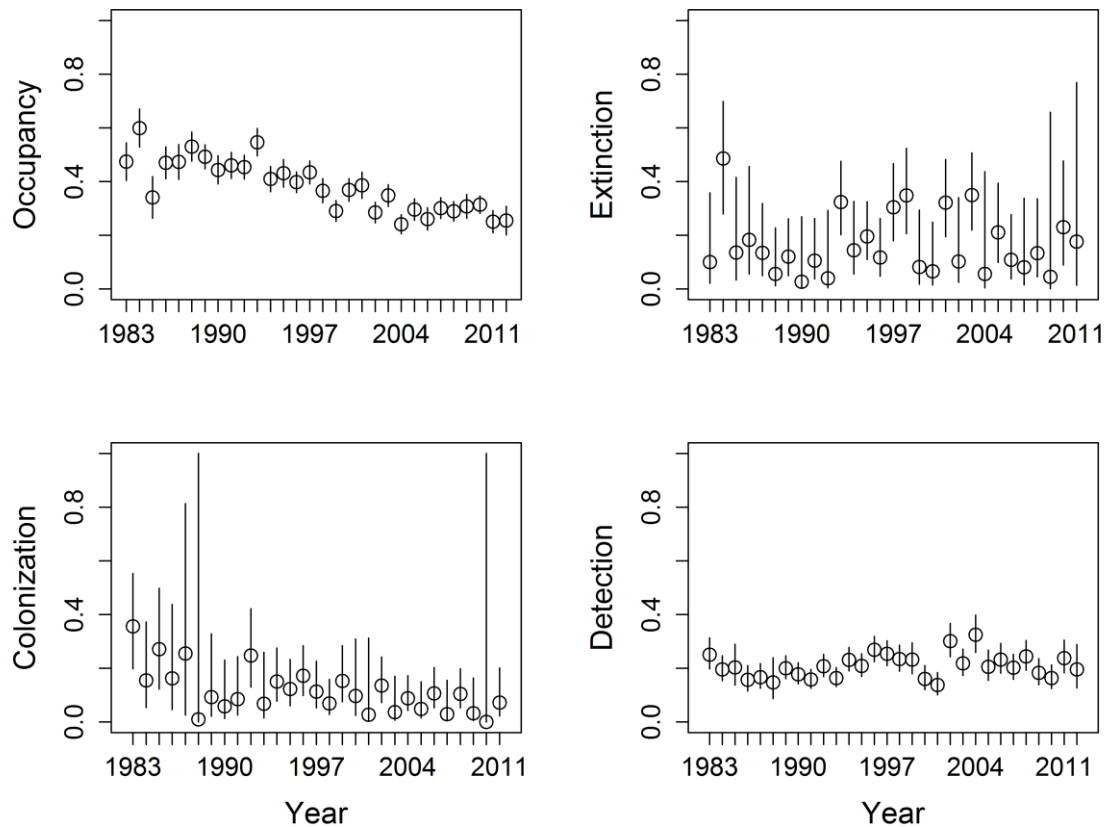
Figure 3.8.1 Annual occupancy, extinction, colonization and detection probability estimates for the Golden-winged Warbler using model-averaged estimates across the top 6 models (see Appendix Table X). Extinction parameter is predicted using Blue-winged Warbler covariate set to not-detected, and in all cases temperature and NDVI are held at their mean value. Error bars represent 95% confidence intervals based on asymptotic standard errors. Occupancy probability standard error estimates are based on nonparametric bootstrapping (500 replicates).
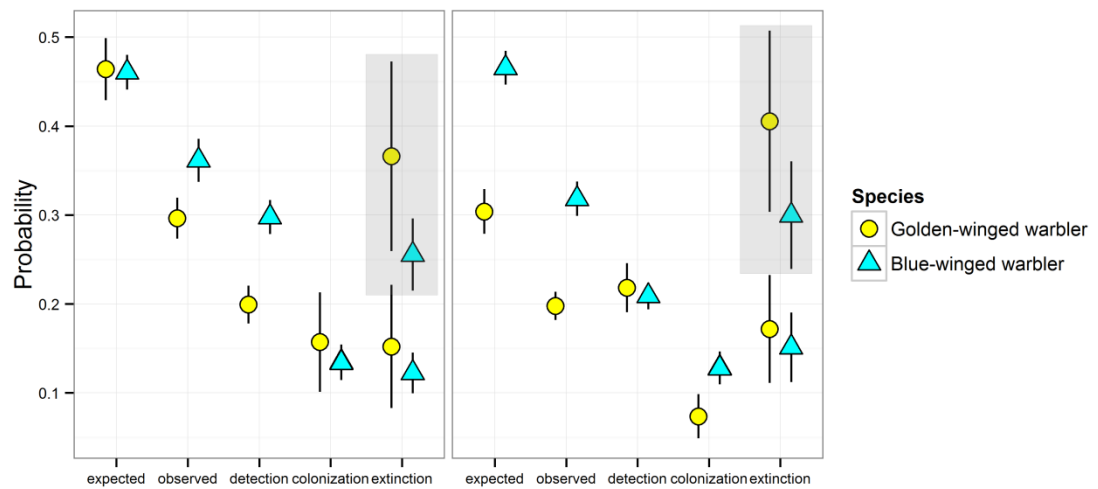
Figure 3.8.2 Dynamic occupancy parameters averaged over two time periods, 1983-1997 (left) and 1998-2012 (right, to 2011 for extinction and colonization parameters) for Golden-winged and Blue-winged Warblers based on estimates of top ranked models. Both colonization and extinction were predicted and averaged separately when the occurrence of the other species was not-detected or detected (gray boxes).
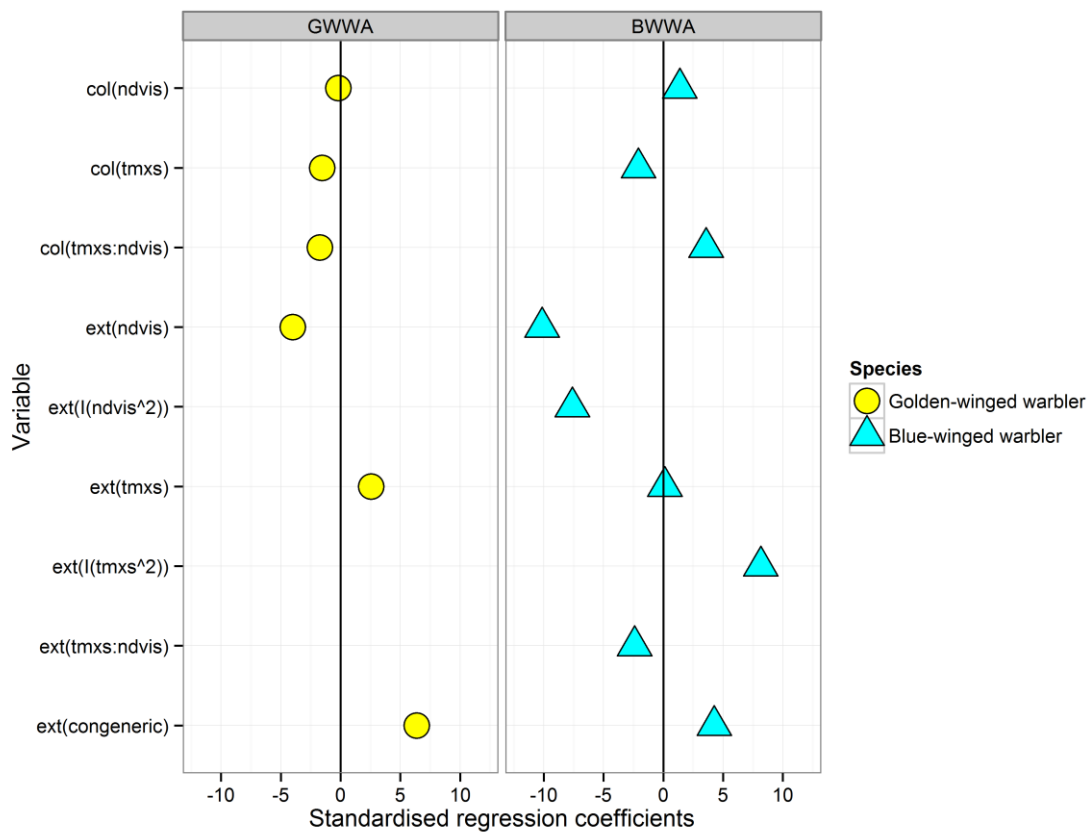
Figure 3.8.3 Standardised regression coefficients for colonization and extinction estimates of the top-ranked dynamic occupancy models for the Golden-winged (GWWA) and Blue-winged Warblers (BWWA).
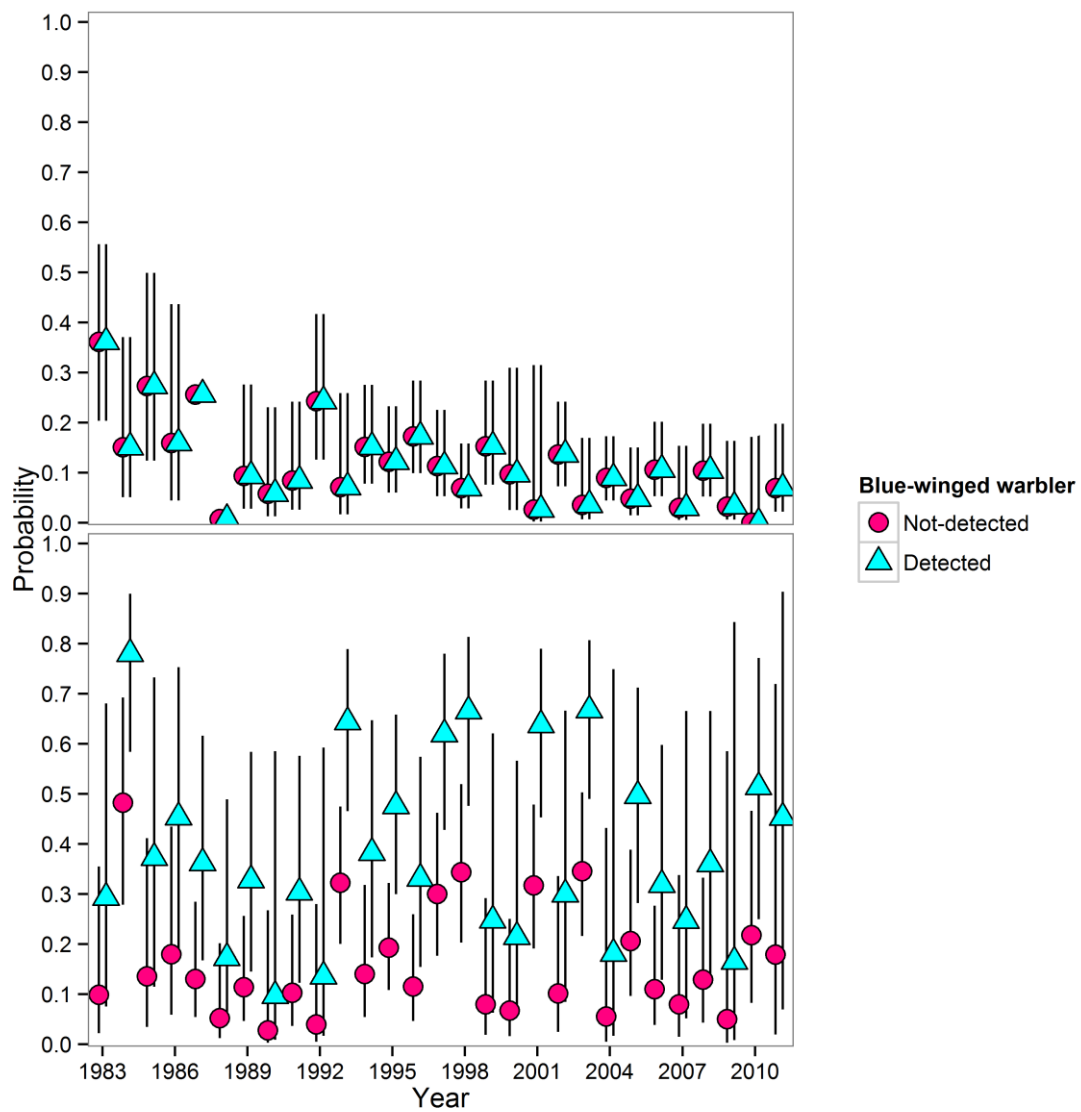
Figure 3.8.4 Comparison of annual estimates of colonization (top) and extinction (bottom) probabilities for the Golden-winged Warbler when Blue-winged Warbler was detected (●) and not-detected (▲).
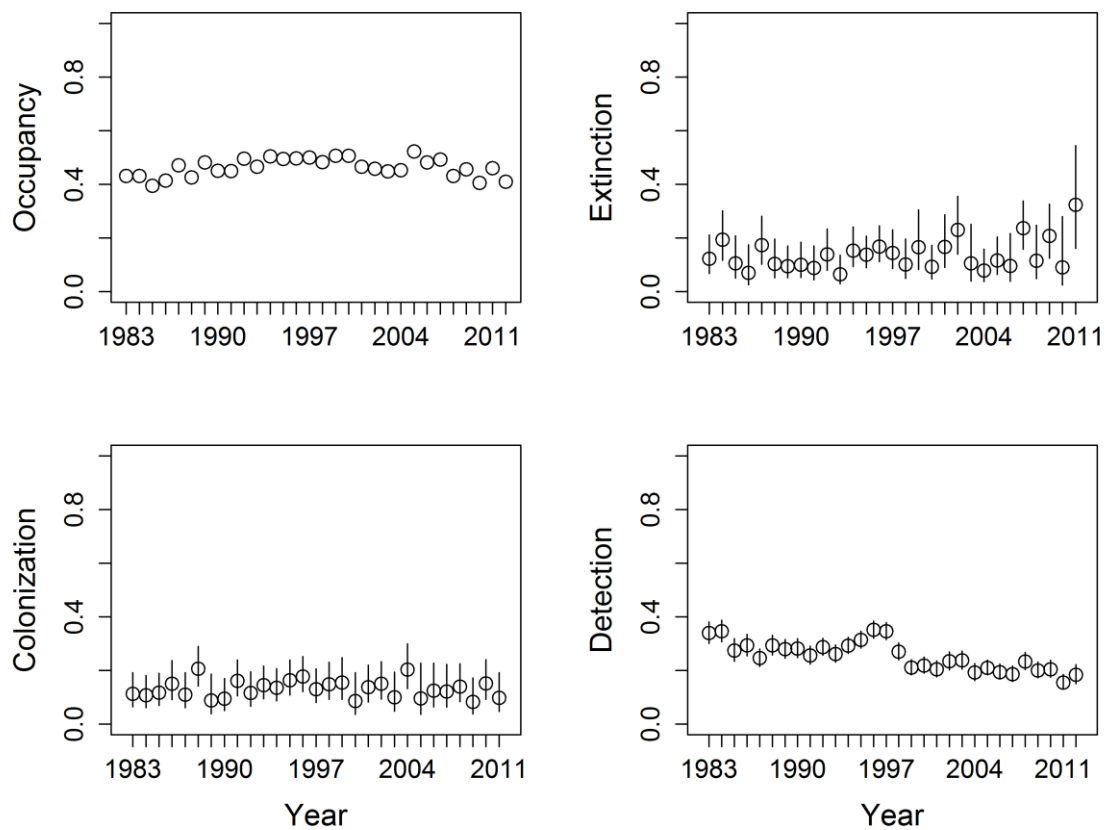
Figure 3.8.5 Annual occupancy, extinction, colonization and detection probability estimates for the Blue-winged Warbler. Extinction parameter is predicted using Blue-winged Warbler covariate set to not detected (0).
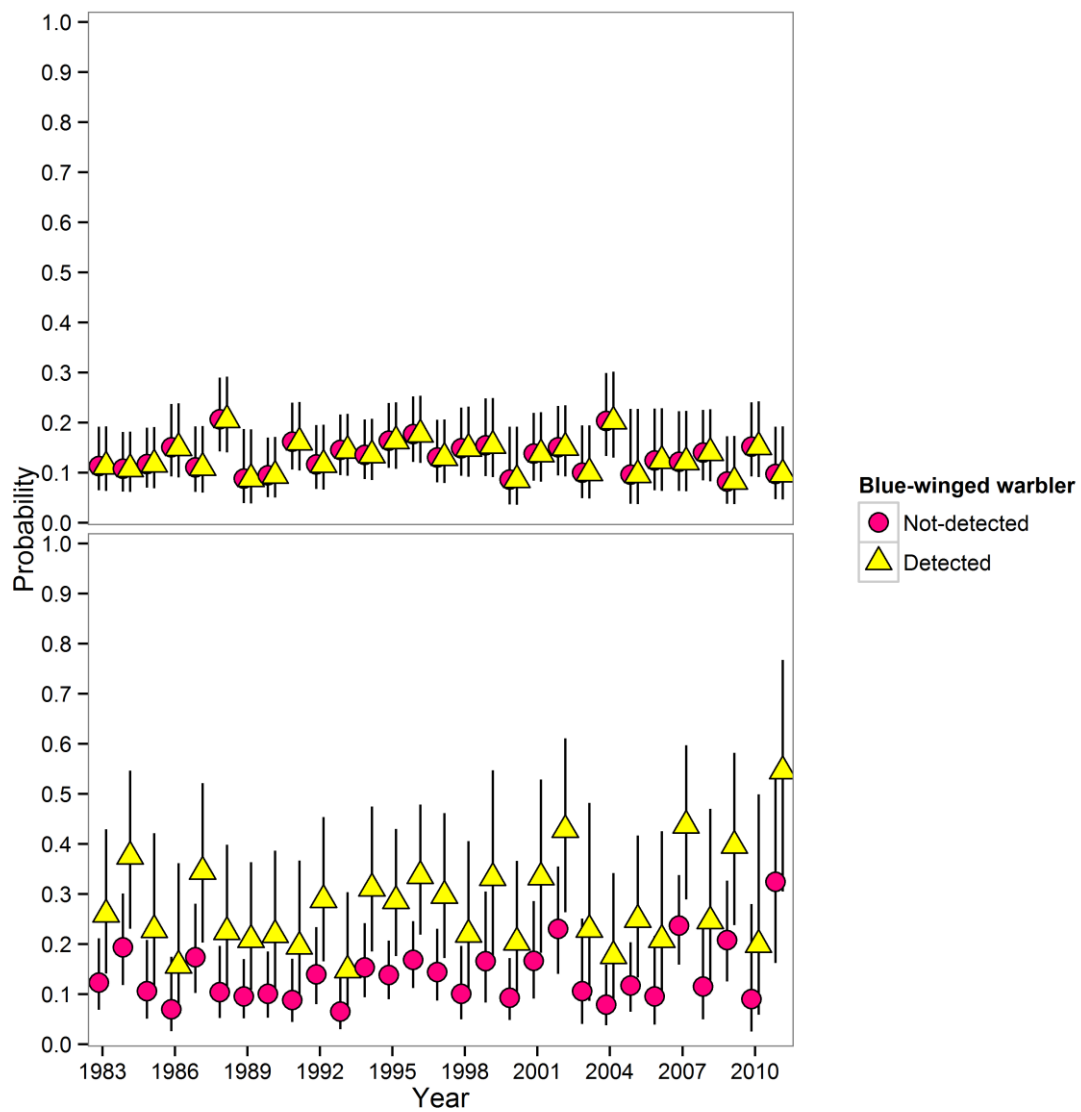
Figure 3.8.6 Comparison of annual estimates of colonization (top) and extinction (bottom) probabilities for the Blue-winged Warbler when Golden-winged Warbler was detected (●) and not-detected (▲).
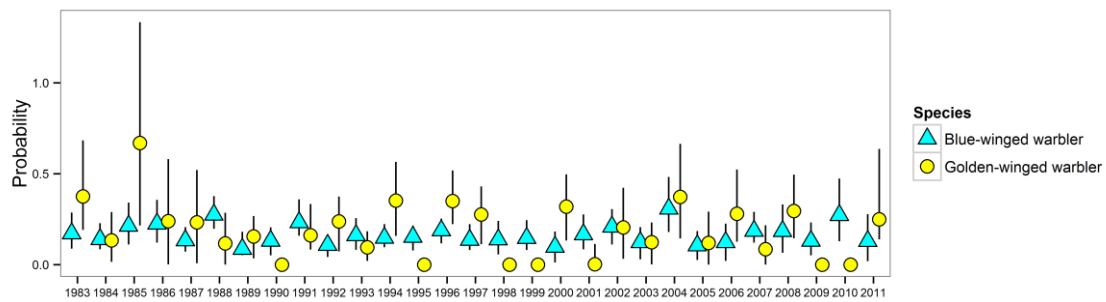
Figure 3.8.7 Range-wide annual mean turnover estimates with 95% confidence intervals based on 1000 bootstrapped samples for the Golden-winged and Blue-winged Warblers.
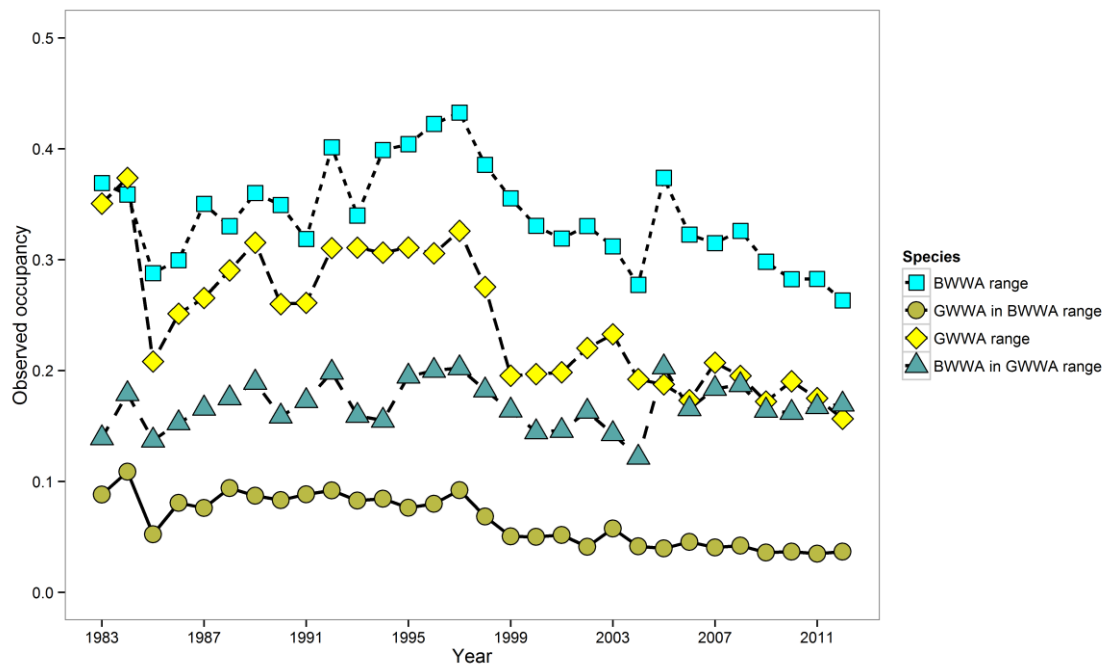
Figure 3.8.8 Naïve occupancy estimates for the Golden-winged Warbler (GWWA) and Blue-winged Warbler (BWWA) in their respective ranges between 1983 and 2012, and proportion of occupied sites of each species intersecting the range boundaries of the opposing species.
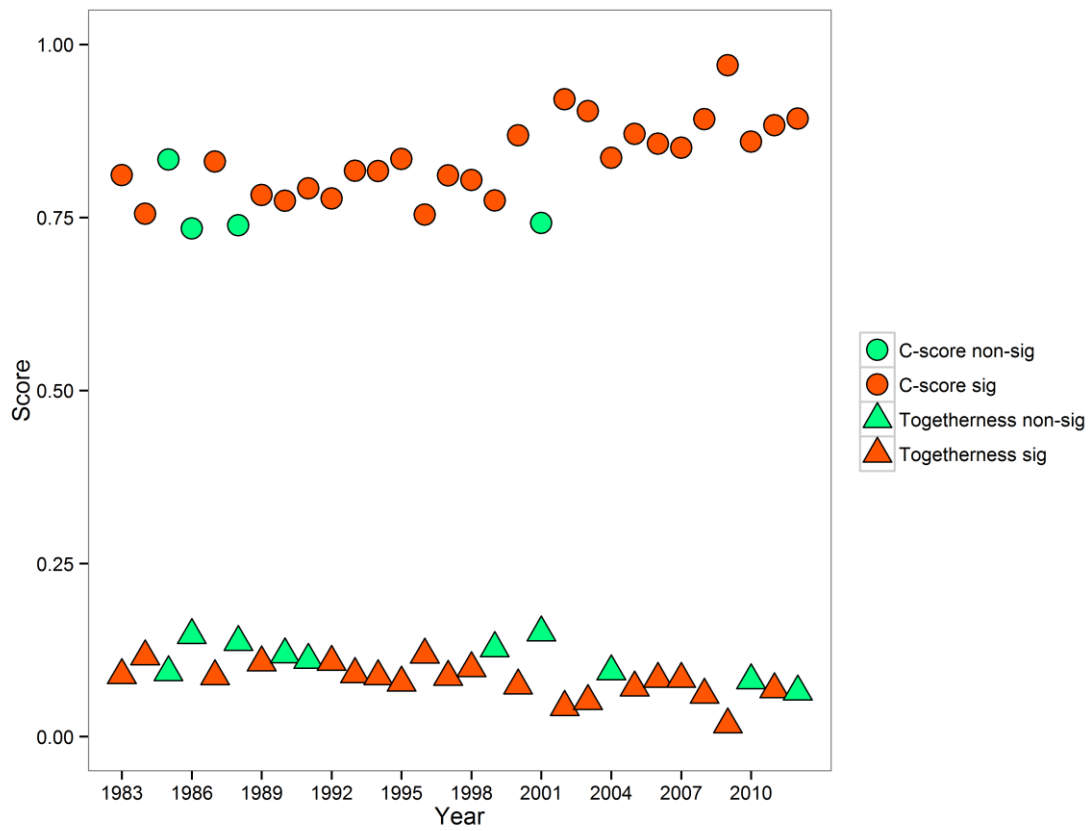
Figure 3.8.9 Inter-annual variation in the normalised C-score and togetherness metric between the Golden-winged Warbler and Blue-winged Warbler.
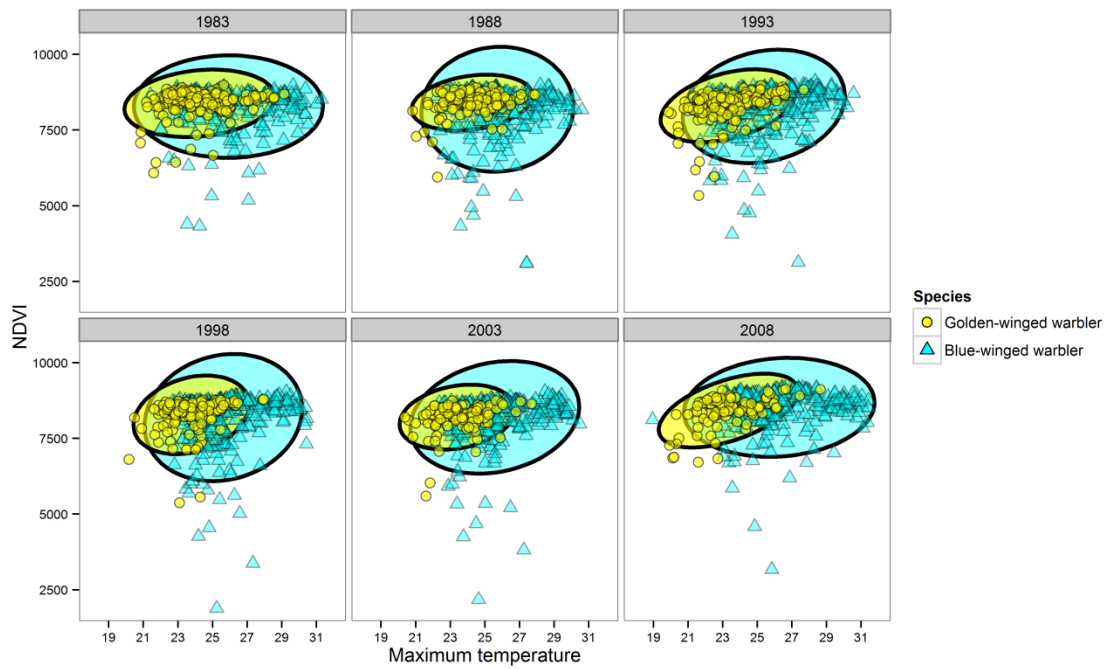
Figure 3.8.10 Niche overlap between the Golden-winged and Blue-winged Warblers with a 95% confidence interval identifying niche boundaries. Values were averaged over the 1983 to 2012 sampling period across the complete range of each species, separately.
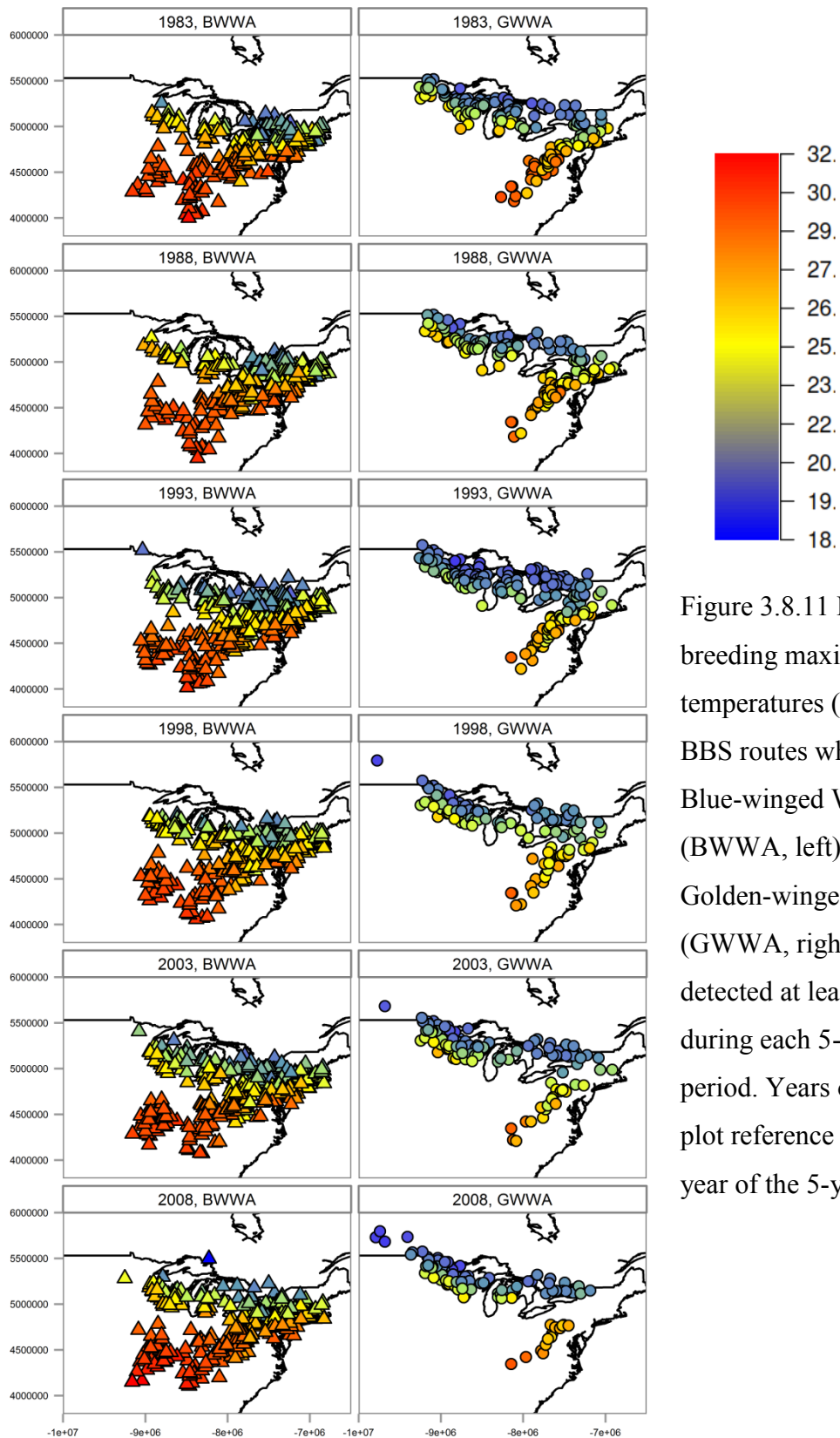
Figure 3.8.11 Mean of breeding maximum temperatures (°C) across BBS routes where the Blue-winged Warbler (BWWA, left) and Golden-winged Warbler (GWWA, right) were detected at least once during each 5-year period. Years on each plot reference the first year of the 5-year period.
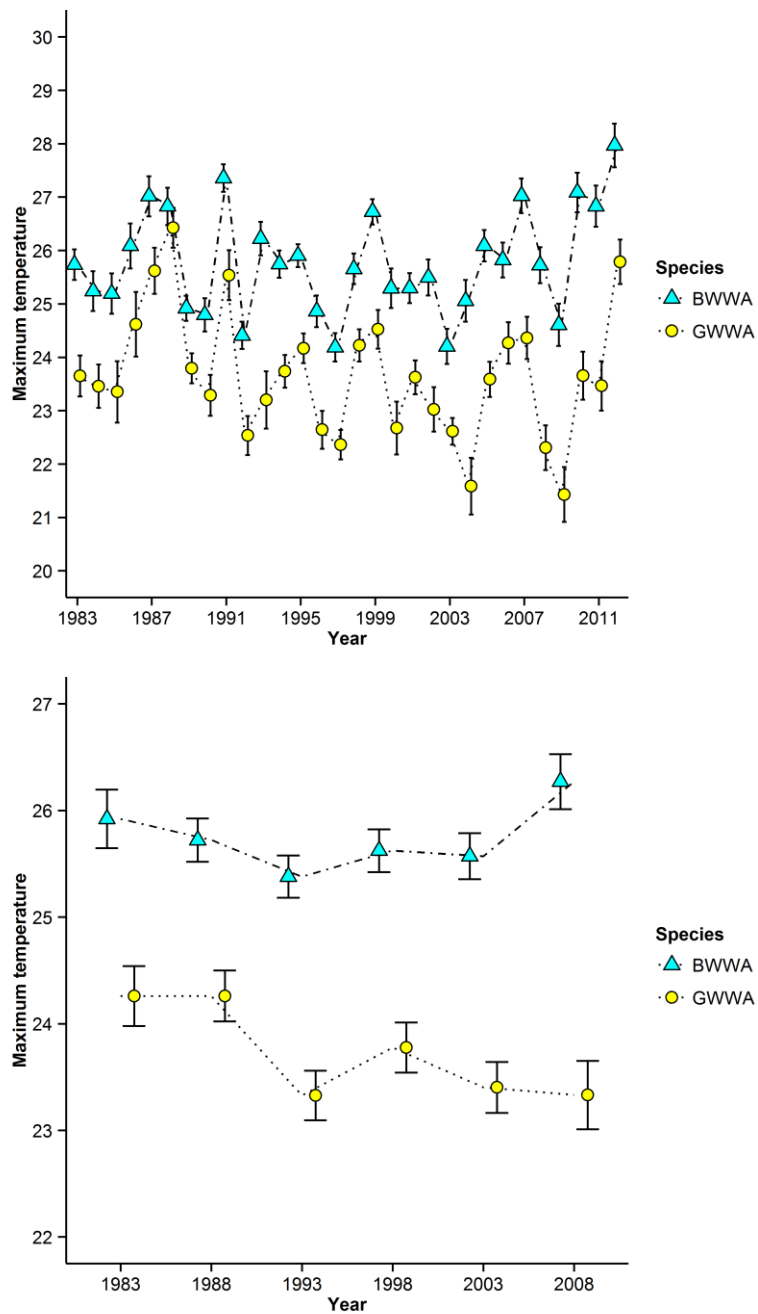
Figure 3.8.12 Annual (top) and 5-year (bottom) means of breeding season maximum temperatures from 1983 and 2012 for the Golden-winged (●) and the Blue-winged (▲) Warbler. Errors bars represent 95% confidence intervals.
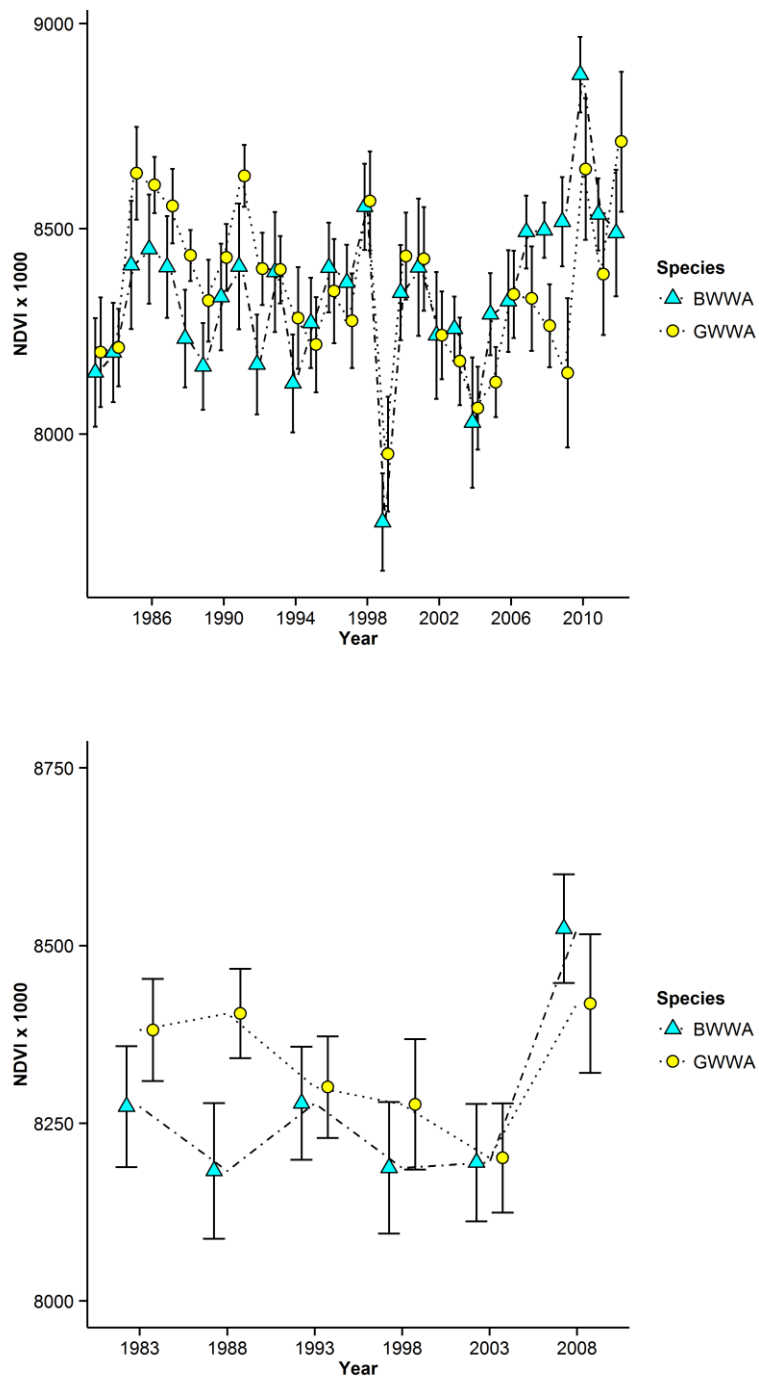
Figure 3.8.13 Annual (top) and 5-year (bottom) means of breeding season NDVI from 1983 and 2012 for the Golden-winged (●) and the Blue-winged (▲) Warbler. Errors bars represent 95% confidence intervals.

3.9 Appendix

3.9.1 Tables

Table 3.9.1 Model fit statistics for Golden-winged Warbler maximum likelihood dynamic occupancy models.

Model	No. of parameters	AIC	Delta AIC	AIC weight	Cumulative weight	Negative log-likelihood	Model code
~1 ~ (year - 1) + tmxs + ndvis + tmxs * ndvis ~ (year - 1) + tmxs + ndvis + bwcov ~ (year - 1) + jul	96	16893.72	0	1.90E-01	0.19	8350.86	m75bw
~1 ~ (year - 1) + tmxs + ndvis + tmxs * ndvis ~ (year - 1) + tmxs + ndvis + tmxs * ndvis + bwcov ~ (year - 1) + jul	97	16894.58	0.86	1.20E-01	0.31	8350.289	m89bw
~1 ~ (year - 1) + tmxs + ndvis + tmxs * ndvis ~ (year - 1) + tmxs + ndvis + I(tmxs^2) + bwcov ~ (year - 1) + jul	97	16894.97	1.25	9.90E-02	0.41	8350.486	m91bw
~1 ~ (year - 1) + tmxs + ndvis + tmxs * ndvis ~ (year - 1) + tmxs + ndvis + I(ndvis^2) + bwcov ~ (year - 1) + jul	97	16895.58	1.86	7.40E-02	0.48	8350.788	m90bw
~1 ~ (year - 1) + tmxs + ndvis + tmxs * ndvis ~ (year - 1) + tmxs + ndvis + bwcov + ndvis * bwcov ~ (year - 1) + jul	97	16895.64	1.92	7.10E-02	0.55	8350.821	m96bw
~1 ~ (year - 1) + tmxs + ndvis + tmxs * ndvis ~ (year - 1) + tmxs + ndvis + bwcov + tmxs * bwcov ~ (year - 1) + jul	97	16895.7	1.98	6.90E-02	0.62	8350.852	m95bw
~1 ~ bwcov ~ bwcov ~ jul	7	16975.7	82.04	2.80E-	1	8480.88	m27bw

Model	No. of parameters	AIC	Delta AIC	AIC weight	Cumulative weight	Negative log-likelihood	Model code
		6		19			
~1 ~ 1 ~ year - 1 ~ year - 1	61	17104.4	210.68	3.30E-47	1	8491.201	m3
~1 ~ 1 ~ 1 ~ year	33	17114.38	220.66	2.30E-49	1	8524.188	m1
~1 ~ year - 1 ~ year - 1 ~ year - 1	89	17129.8	236.08	1.00E-52	1	8475.902	m4
~1 ~ 1 ~ 1 ~ 1	4	17136.66	242.94	3.30E-54	1	8564.331	m0
~1 ~ year - 1 ~ 1 ~ year – 1	61	17181.83	288.11	5.10E-64	1	8529.913	m2

Table 3.9.2 Model fit statistics for maximum likelihood based dynamic occupancy models for the Blue-winged Warbler Models in bold were within 2 AIC from the top ranked model

Model	No. of parameters	AIC	Delta AIC	AIC weight	Cumulative weight	Negative log-likelihood
~t1 + n1 + I(n1^2) + I(t1^2) gamma~ (year - 1) + tmxs + ndvis + tmxs * ndvis ~ (year - 1) + tmxs + ndvis + I(ndvis^2) + I(tmxs^2) + tmxs * ndvis + gwcov + ~ (year - 1) + jul	104	41376.09	0	9.90E-01	0.99	20584
~1 gamma~ gwcov ~ gwcov ~ jul	7	41868.78	492.7	1.00E-107	1	20927.4
~1 gamma~ 1 ~ 1 ~ year	33	41996.4	620.32	2.00E-135	1	20965.2
~1 gamma~ year - 1 ~ 1 ~ year - 1	61	42025.56	649.47	9.20E-142	1	20951.8
~1 gamma~ year - 1 ~ year - 1 ~ year - 1	89	42042.42	666.3	2.00E-	1	20932.2

Model	No. of parameters	AIC	Delta AIC	AIC weight	Cumulative weight	Negative log-likelihood
			4	145		
~1 gamma~ 1 ~ year - 1 ~ year - 1	61	42051.36	675.27	2.30E-147	1	20964.7
~1 gamma~ 1 ~ 1 ~ 1	4	42199.46	823.37	1.60E-179	1	21095.7

3.9.2   Figures
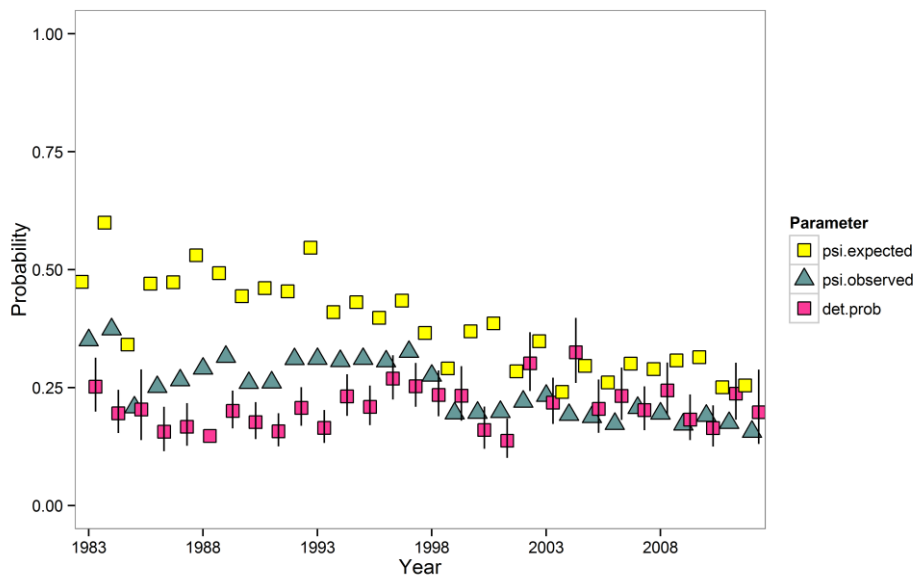
Figure 3.9.1 Naïve (▲) and expected (□) occupancy estimates and detection probability between 1983 and 2012 for the Golden-winged Warbler across its complete range.
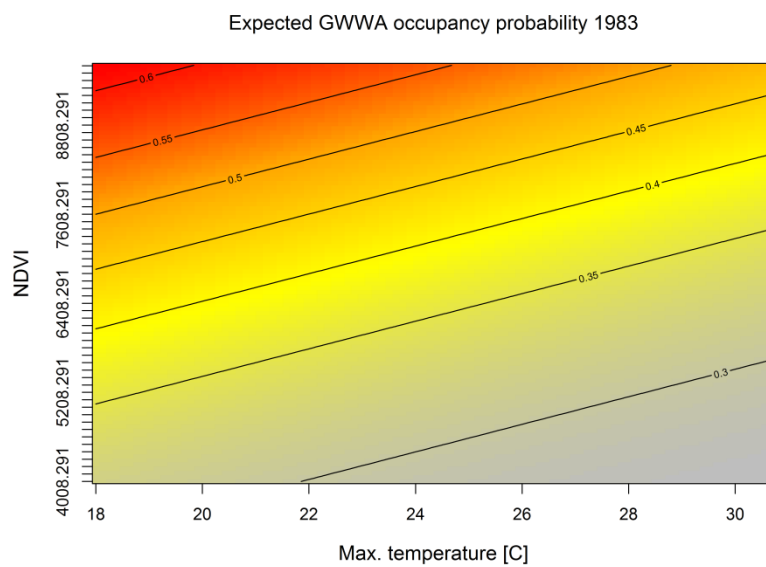
Figure 3.9.2 First-year occupancy probability, Golden-winged Warbler
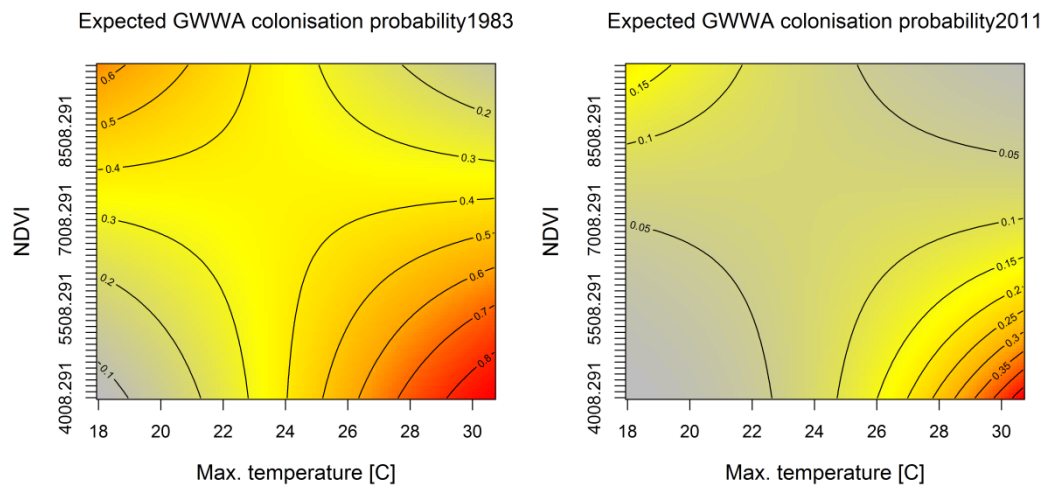
Figure 3.9.3 Colonization probability 1983 (left) and 2011 (right).
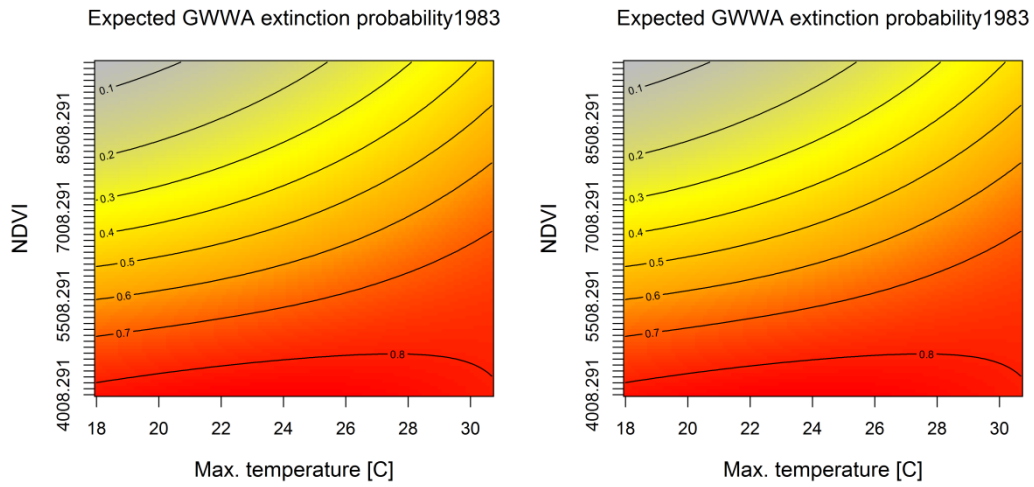
Figure 3.9.4 Extinction probability1983. BBWA not detected (left) and BWWA detected (right)
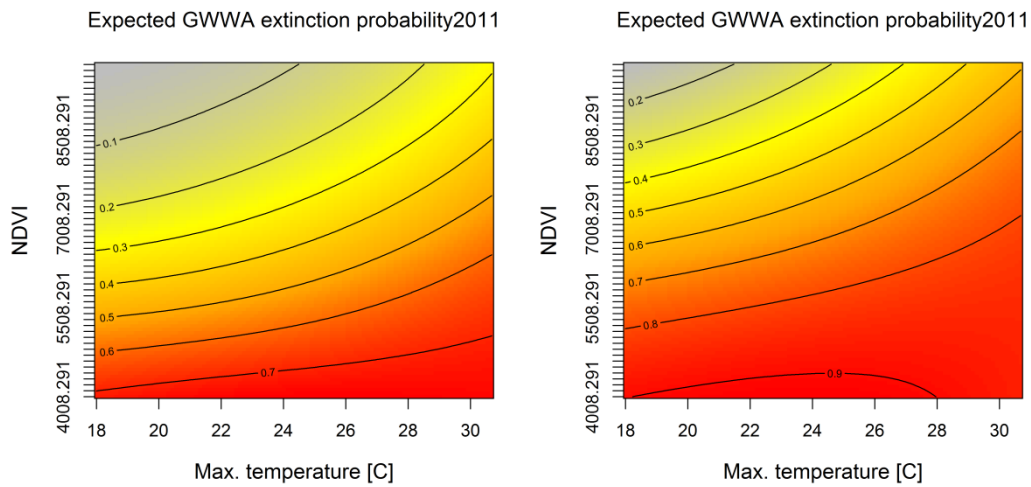
Figure 3.9.5 Extinction probability 2011. BBWA not detected (left) and BWWA detected (right)
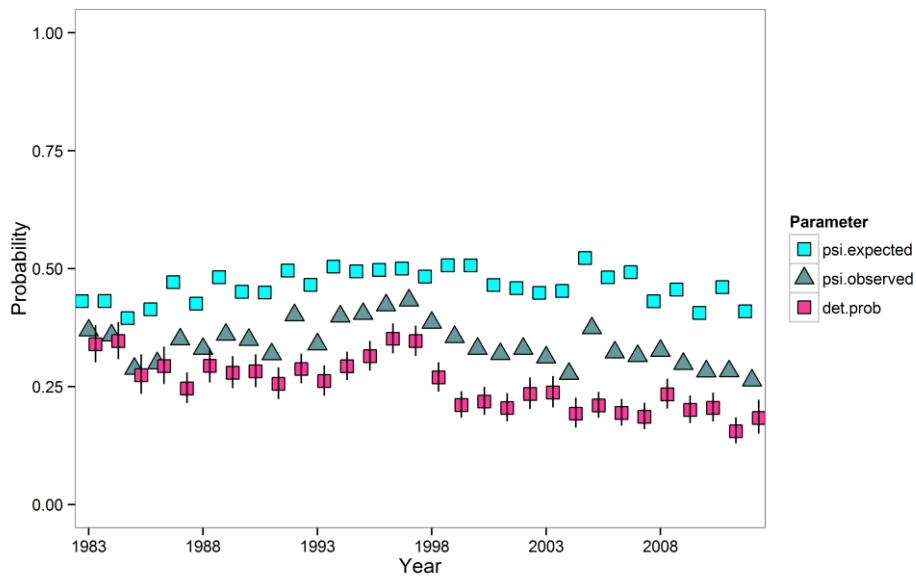
Figure 3.9.6 Naïve (▲) and expected (□) occupancy estimates and detection probability between 1983 and 2012 for the Blue-winged Warbler across its complete range.
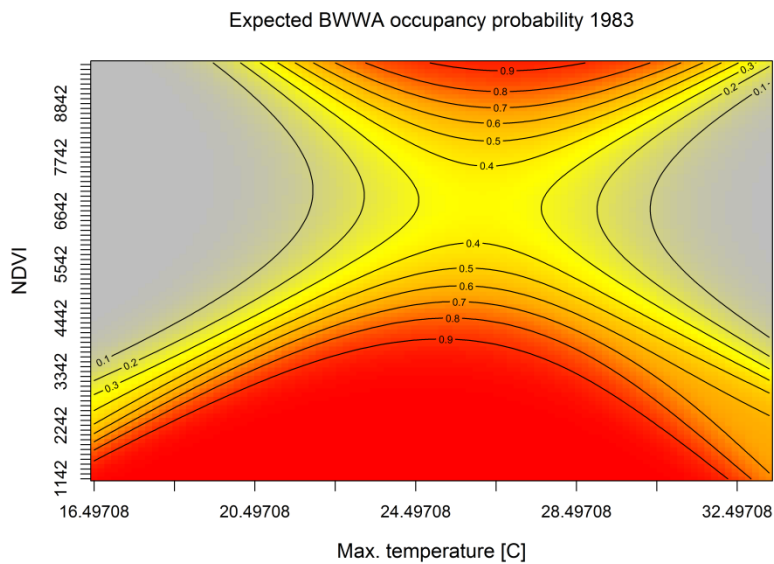
Figure 3.9.7 First year occupancy probability, Blue-winged Warbler
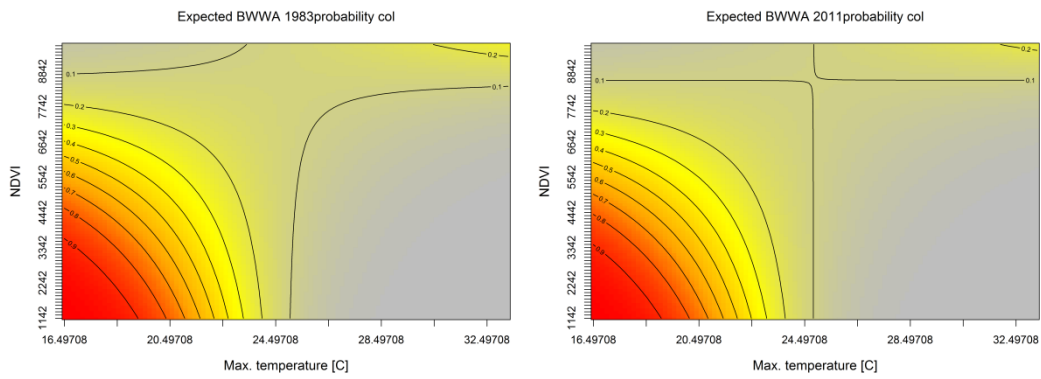
Figure 3.9.8 Colonization probability 1983 (left) and 2011 (right), Blue-winged Warbler.
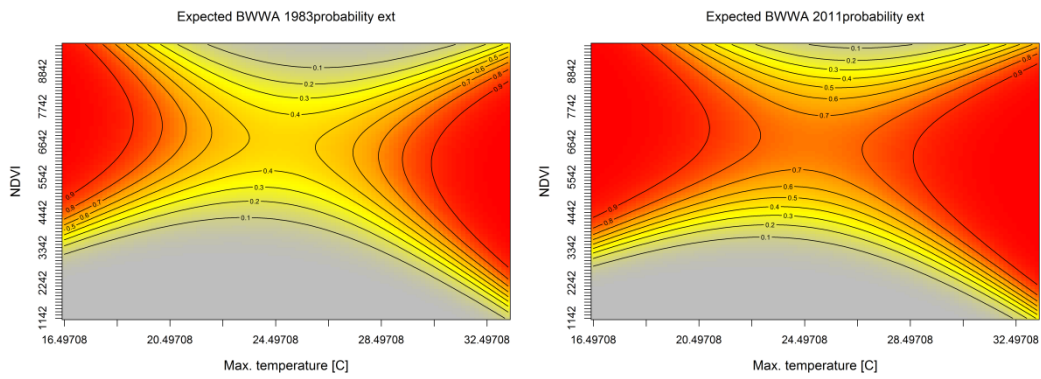
Figure 3.9.9 Extinction probability predictions for the Blue-winged Warbler for 1983 (left) and 2011 (right), when Golden-winged Warbler was detected.
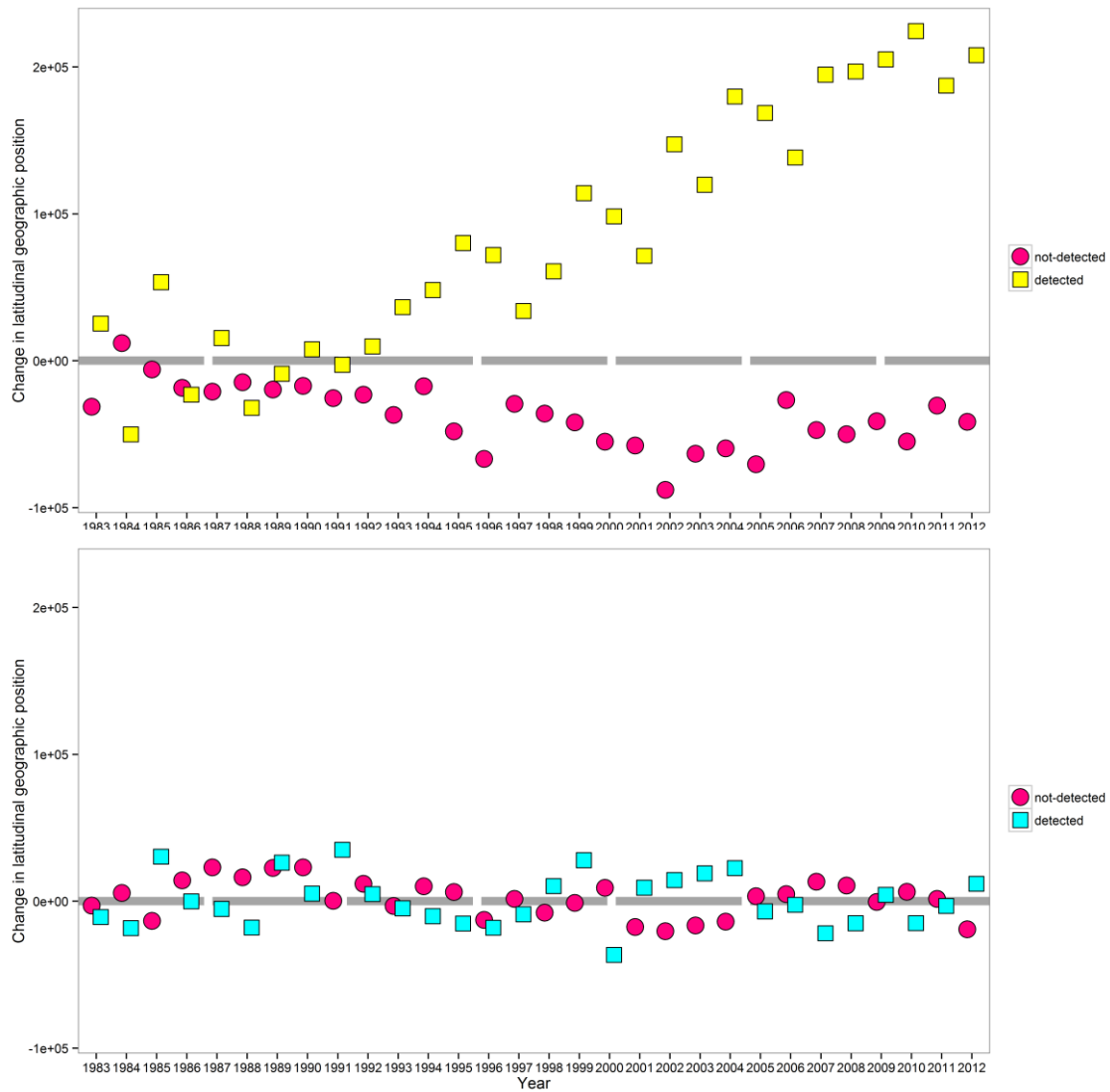
Figure 3.9.10 Contrasting spatio-temporal range dynamics, based on North American Breeding Bird Survey detection and non-detection data, of the Golden-winged (upper plot) and the Blue-winged Warbler (lower plot), with the former exhibiting strong northern latitudinal shifts of detections. Differences were calculated from the mean latitudinal centroid of the range (hashed gray line).
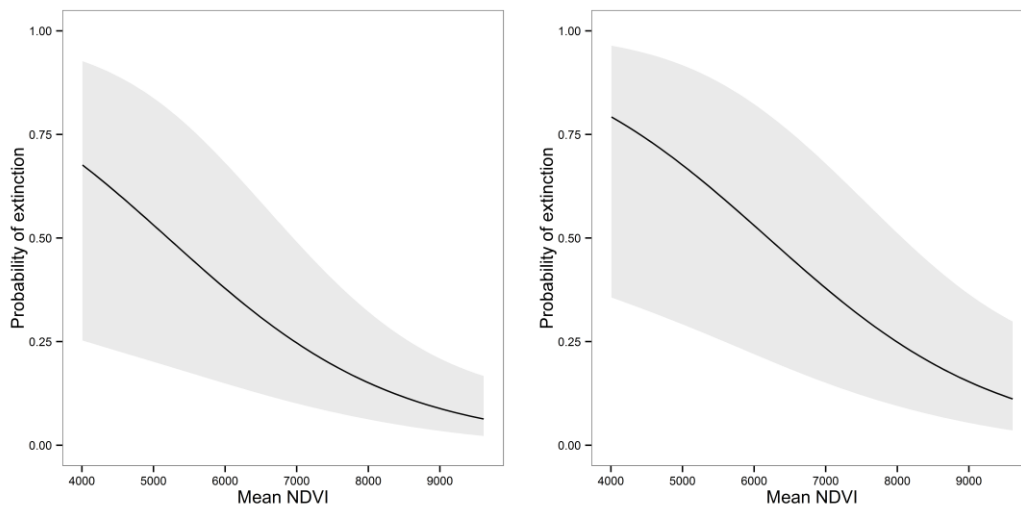
Figure 3.9.11 Golden-winged Warbler predicted probability of extinction as a function of mean seasonal NDVI, model-averaged predictions for 1983 (left) and 2011 (right), Blue-winged Warbler covariate set to not-detected.
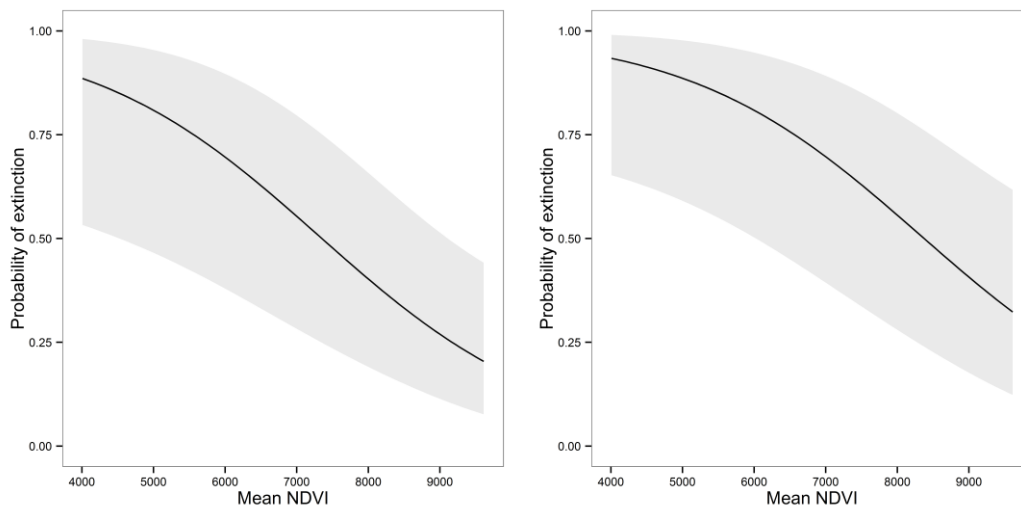
Figure 3.9.12 Golden-winged Warbler predicted probability of extinction as a function of mean seasonal NDVI, model-averaged predictions for 1983 (left) and 2011 (right), Blue-winged Warbler covariate set to detected.
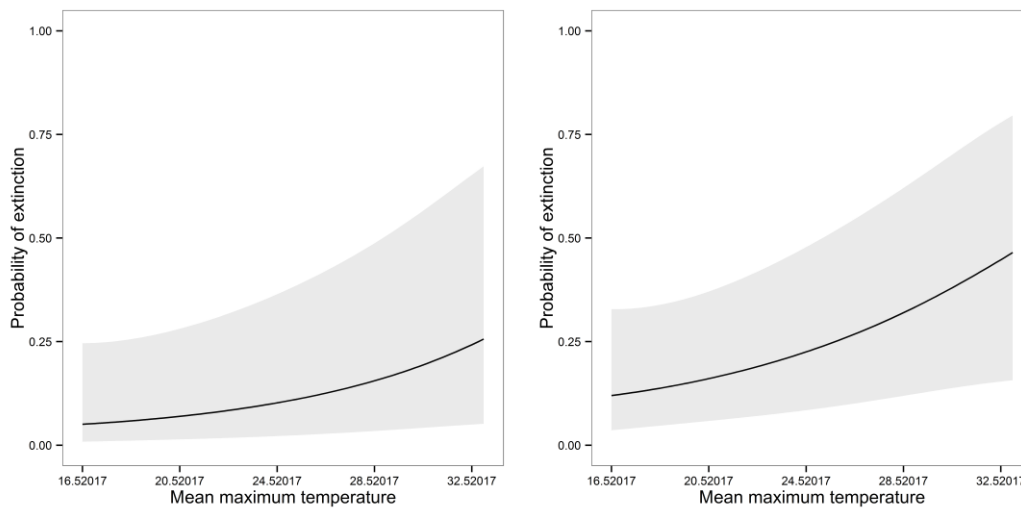
Figure 3.9.13 Golden-winged Warbler predicted probability of extinction as a function of maximum seasonal temperature, model-averaged predictions for 1983 (left) and 2011 (right), Blue-winged Warbler covariate set to not-detected.
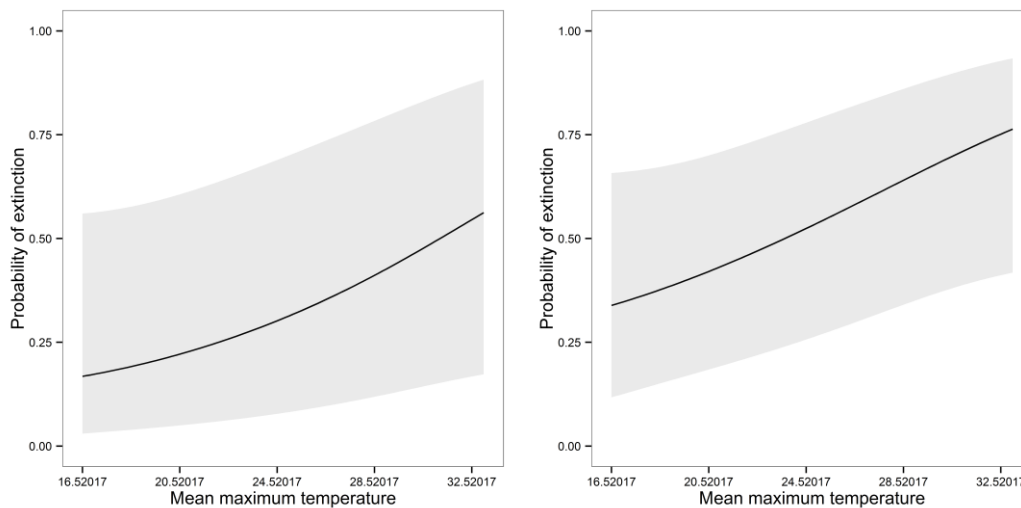
Figure 3.9.14 Golden-winged Warbler probability of extinction as a function of maximum seasonal temperature, model-averaged predictions for 1983 (left) and 2011 (right), Blue-winged Warbler covariate set to detected. Gray regions represent 95% confidence intervals.
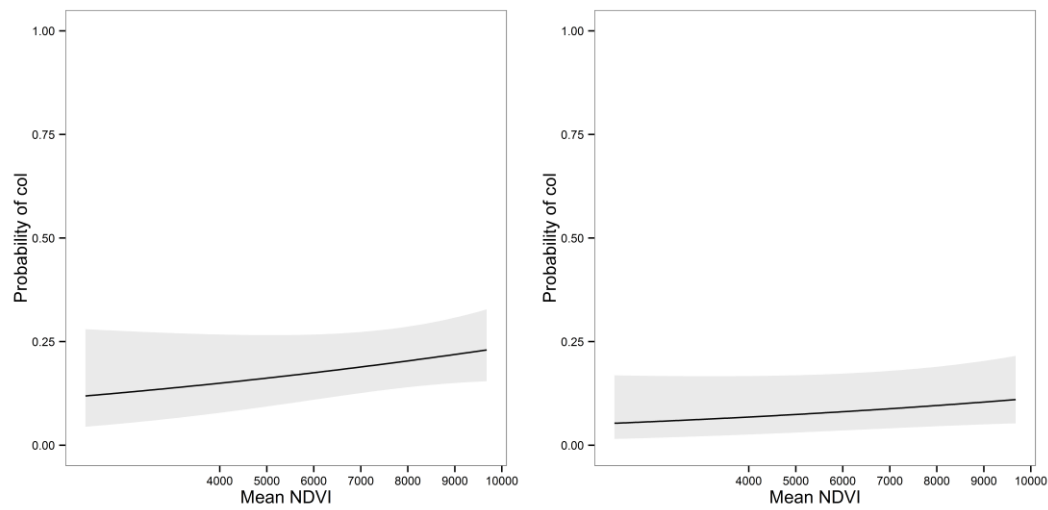
Figure 3.9.15 Blue-winged Warbler predicted probability of colonization as a function of mean seasonal NDVI 1983 (left) and 2011 (right). Gray regions represent 95% confidence intervals.
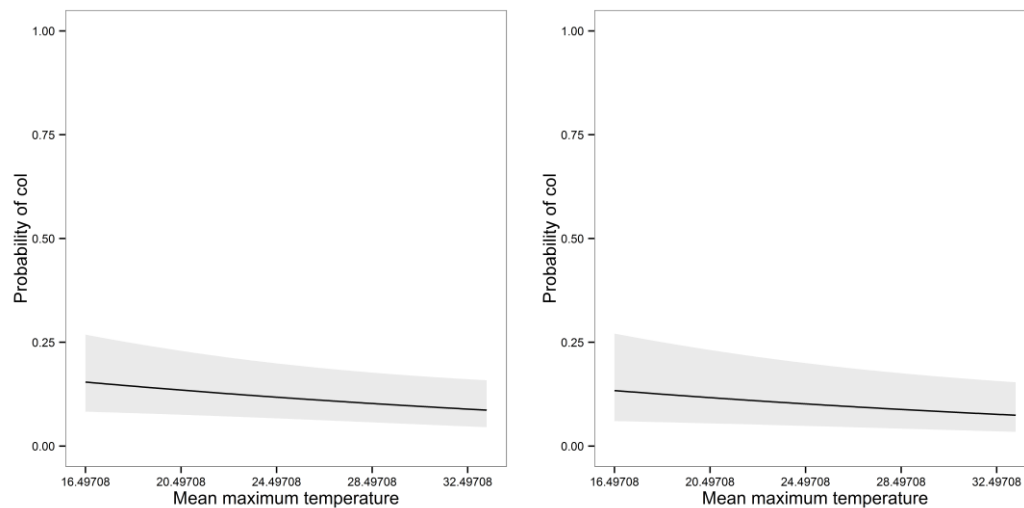
Figure 3.9.16 Blue-winged Warbler predicted probability of colonization as a function of maximum seasonal temperature for 1988 (left) and 2011 (right). Gray regions represent 95% confidence intervals.
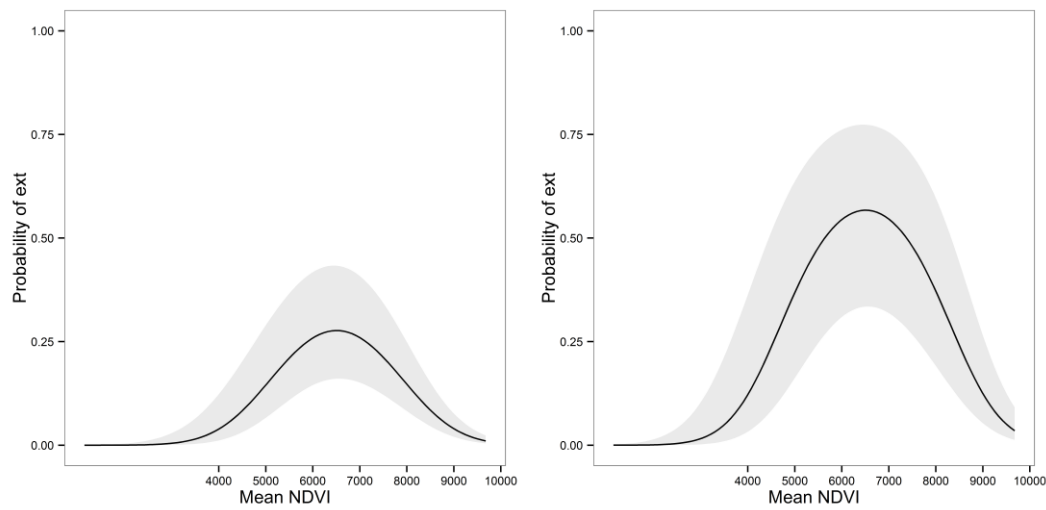
Figure 3.9.17 Blue-winged Warbler predicted extinction probability as a function of mean seasonal NDVI for 1983 (left) and 2011 (right). Golden-winged Warbler detections were set to non-detected. Gray regions represent 95% confidence intervals.

Figure 3.9.18 Blue-winged Warbler predicted extinction probability as a function of maximum seasonal temperature for 1983 (left) and 2011 (right). Golden-winged Warbler covariate were set to non-detected. Gray regions represent 95% confidence intervals.

Chapter 4

4 Relevance of uncertainties in coupled species distribution-metapopulation dynamics models for risk assessments under climate change

4.1 Abstract

4.1.1 Aim

Species distribution models (SDMs) coupled with metapopulation dynamics models can integrate multiple threats and population-level processes that influence species distributions. However, multiple sources of uncertainties could lead to substantial differences in model outputs and jeopardize risk assessments. We evaluate uncertainties in coupled SDM-metapopulation models and focus on two often under-appreciated sources of uncertainty: the choice of general circulation model (GCM) and parameter uncertainty of the metapopulation model. We rank the risks associated with potential climate changes and habitat loss on projected range margin dynamics of the Hooded Warbler (*Setophaga citrina*).

4.1.2 Location

Breeding range of the Hooded Warbler, North America

4.1.3   Methods

Using SDMs we quantified variability in projected future distributions using four GCMs and a consensus model at the biogeographic scale and assessed the propagation of uncertainty through to metapopulation viability projections. We applied a global sensitivity analysis to the coupled SDM-metapopulation model to rank the influence of choice of GCM, parameter uncertainty, and simulated effects of habitat loss on metapopulation viability, thereby addressing error propagation through the whole modeling process.

4.1.4   Results

The Hooded Warbler range was consistently projected to shift north: choice of GCMs influenced the magnitude of change and variability was spatially structured. Variability in the choice of GCMs propagated through to metapopulation viability projections, highlighting potential biases when using a single GCM. Although viability measures were sensitive to the GCM used, measures of direct habitat loss were more influential.

4.1.5   Main conclusions

This work underscores the importance of a global sensitivity analysis framework applied to coupled models to disentangle the relative influence of uncertainties on projections. The use of multiple GCMs enabled the exploration of a range of possible outcomes relative to the consensus GCM, helping to inform risk estimates. Ranking uncertainties informs the prioritization of management actions for species affected by dynamic anthropogenic threats over multiple spatial scales.

4.1.6   Key words

Population viability analysis, multiple threats, range margins, species distribution model, sensitivity analysis, uncertainty

4.2   Introduction

Correlative species distribution models (SDMs; e.g. habitat suitability models, bioclimatic envelope models) provide a first pass assessment of the potential for future climate changes to influence range dynamics (Huntley *et al.*, 2008, Doswald *et al.*, 2009, Lawler *et al.*, 2009). While SDMs are likely to remain a useful tool for assessing the potential risks of climate change (Garcia *et al.*, 2011), however, their limitations (Guisan & Thuiller, 2005, Araújo & Peterson, 2012) and potential to bias risk estimates (Fordham *et al.*, 2012a) have heralded the need for increased use of multi-modelling frameworks that incorporate dynamic processes that directly influence species distributions and abundances (Brook *et al.*, 2009, Franklin, 2010, Huntley *et al.*, 2010). One increasingly used approach includes SDMs coupled with spatially structured metapopulation dynamics models (Lawson *et al.*, 2010, Aiello-Lammens *et al.*, 2011, Conlisk *et al.*, 2012). These coupled models are a powerful simulation and decision support tool that can be used to assess the effect of global changes such as climate changes and land use conversions on species persistence. Applying this modeling approach within a population viability analysis (PVA) framework allows the assessment of threats to species persistence, estimation of extinction risk, and ranking of management scenarios (Akçakaya & Burgman, 1995). One of the key limitations of coupled SDM-metapopulation dynamics models, however, are the numerous sources of uncertainty that are rarely considered (Ruete *et al.*, 2012) but can be propagated through the coupled models and projections.

Uncertainty associated with coupled SDM-metapopulation dynamics models may impact model projections and potentially compromise management decisions and climate change adaptation strategies. When used to assess global climate changes on extinction risk, different types of uncertainties are associated with each constituent model including the SDM, choice of general circulation models (GCMs) used to simulate future climates, and the metapopulation dynamics model (Fig. 4.8.1). Common sources of uncertainty in ecology include the choice of modeling approach and structure, inability to adequately capture natural variation (parameter uncertainty), and systematic biases (Regan *et al.*, 2002). Coupled SDM- metapopulation dynamics models are typically used in a hierarchical framework; the SDM and the subsequent projections under future climate change scenarios (or land cover change) form the spatially and temporally dynamic patch structure on which the metapopulation dynamics model is based

(Akçakaya *et al.*, 2004). Thus uncertainties associated with each component of the model chain (Fig. 4.8.1) have the potential to proliferate through to forecasted species viability outcomes. While such models are useful to derive better hypotheses regarding processes relevant to species range shifts, quantifying uncertainties from each constituent model is essential to provide a comprehensive risk assessment and to support robust management decisions.

Differences in projections of suitable habitats resulting from variability across GCMs are important to consider when predicting the response of populations occurring along range margins to potential climate changes. These range edge populations are of interest because novel climatic conditions can either favor a species' range expansion or diminish it. Variability of different climate models can influence the magnitude, direction, and rates of change in projections of suitable climate space (Buisson *et al.*, 2010, Grenouillet *et al.*, 2011), and has the potential to influence the outcome of targeted management in these regions. There is a high degree of variability among GCMs within an emission scenario that may differ depending on the climate variable under consideration, which can result in different directions of change for simulated future variables (Tebaldi & Knutti, 2007, Fordham *et al.*, 2011). The uncertainty associated with choice of GCMs has been more thoroughly explored using SDMs (Diniz-Filho *et al.*, 2009, Buisson *et al.*, 2010, Garcia *et al.*, 2011, Albouy *et al.*, 2012). Though, the effect of GCM variability on population projections has not been the explicit focus of studies using coupled SDM-PVA models (e.g, Ruete *et al.*, 2012) where typically, coupled SDM- metapopulation dynamics models apply one or two GCMs (Anderson *et al.*, 2009, Lawson *et al.*, 2010).

Developing consensus among climate models has been used by climatologists as a way to account for uncertainties associated with different GCMs (Murphy et al., 2004, Knutti et al., 2010), and recently has been adopted by ecologists in risk assessments for biodiversity under potential climate changes (Araújo & New, 2007a, Fordham et al., 2011). As consensus forecasting may reduce variability across all models by deriving the central tendency of forecasts (Araújo & New, 2007a, Pierce et al., 2009, Garcia et al., 2011, Fordham et al., 2012b), there is the potential for the effects of extreme scenarios to be masked (Beaumont *et al.*, 2008). This raises the question of the relevance of consensus techniques for climate change risk assessment.

Metapopulation dynamics models, while biologically more realistic than SDMs, typically necessitate development with simplifying assumptions in large part owing to our lack of knowledge and understanding of ecological systems (Ludwig, 1999, Burgman *et al.*, 2005, Beissinger *et al.*, 2006). Although they integrate demographic and dispersal processes relevant to species dynamics in suitable habitat, the assumptions used in model formulation or parameter uncertainty may further compound the potential cascade of uncertainty through the chain of SDM-PVA models. The importance of uncertainty is often articulated in population dynamics models (Naujokaitis-Lewis *et al.*, 2009), yet it is rare for the full complement of uncertain factors to be varied concurrently (Chu-Agor *et al.*, 2012), and analyzed using a global sensitivity analysis (Saltelli *et al.*, 2006). The advantage of a global sensitivity analysis is that the complete range of plausible parameter values and its impacts on model outcomes may be explored, while varying uncertain parameters simultaneously allows for the identification of potentially important interactions.

The distribution and availability of suitable habitat is likely to be influenced by changes in global climatic conditions and direct loss of habitats associated with anthropogenic disturbances, two processes that may threaten species independently or in combination (Thomas *et al.*, 2004). As climate change is expected to lead to range margin shifts for many species, habitat losses may function as barriers to movement leading to both lowered colonization success and species persistence at the range margins (Travis, 2003, Opdam & Wascher, 2004). Whereas dominant climate changes are the result of fluctuations operating at global scales thus influencing species throughout their range (Thomas, 2010), heterogeneous patterns of habitat loss may be the result of threats operating at regional or landscape levels (Opdam & Wascher, 2004). The impacts of both types of threats and their associated uncertainties can be quantified in process-based metapopulation dynamics models, which enable the integration of dynamic anthropogenic threats that occur over multiple spatial scales.

The aim of this paper is to focus on uncertainties resulting from the choice of GCM and parameter uncertainty of spatial PVAs, two often underappreciated sources of uncertainty (Naujokaitis-Lewis *et al.*, 2009, Fordham *et al.*, 2011) in the context of climate change risk assessment for conservation. We emphasize the importance of these sources of uncertainties for understanding species range dynamics at the expanding range edge margins of the Hooded

Warbler (*Setophaga citrina*) (Melles *et al.*, 2011). To address the variability of GCM projections, we develop SDMs at the scale of the entire breeding range of the Hooded Warbler and project climate changes to the 2080s, using four GCMs. We compare outcomes from individual distribution projections with a consensus forecast and discuss the implications for biodiversity conservation risk assessment under climate change. Through simulation, we model the influence of climate changes and direct loss of habitat on metapopulation dynamics at the range margin. Finally, we apply a global sensitivity analysis (Saltelli *et al.*, 2006) to quantify the influence of parameter uncertainty of a stochastic metapopulation demographic model relative to the risks of climate change and habitat loss. By targeting uncertainty associated with the GCMs and metapopulation dynamics model, our approach enables insights into the relative influence of uncertainties stemming from different steps of the modelling process. We end by discussing the relevance of these uncertainties for management actions in dynamic landscapes.

4.3   Methods

4.3.1   Study system and species

We quantify the relative influence associated with choice of GCMs and parameter uncertainty of the metapopulation dynamics model on the Hooded Warbler, a Nearctic-Neotropical long-distance migratory bird species, whose current breeding distribution occurs throughout the eastern United States and the southern portions of Ontario, Canada (Fig. 4.8.2). This species was selected as it has undergone recent shifts in its northern range margin in part due to recent climate warming (Hitch & Leberg, 2007, Melles *et al.*, 2011). Despite this recent shift, Hooded Warblers are reliant on remnant forested patches that occur throughout the eastern Great Lakes lowland forest and southern Great Lakes forest ecoregions (Olson *et al.*, 2001). However, both of these ecoregions are critically endangered due to the high population densities and dominant agricultural, urban, and industrial land-uses (Ricketts *et al.*, 1999). No significantly sized tracts of forest habitats remain, and the intact forests are highly threatened by land conversion pressures from agriculture and urban sprawl (Ricketts *et al.*, 1999).

4.3.2   Species and climate data

To evaluate the potential consequences of future climate changes on the distribution of the Hooded Warbler, we developed SDMs under current conditions using occurrences across its

complete breeding range (Fig. 4.8.2), capturing the full range of climatic conditions of its niche. Occurrence data were retrieved from the North American Breeding Bird Survey data (BBS; (USGS Patuxent Wildlife Research Center, 2012) and the Ontario Breeding Bird Atlas (OBBA; (Bird Studies Canada *et al.*, 2008) to ensure adequate representation across its entire range, including its northern range limits. BBS occurrence data were compiled for the years 1981-2005 and data that conformed to the BBS standards for weather, date, time, and observer criteria were included. OBBA is a compilation of breeding bird surveys undertaken by volunteers over a five year period every 20 years. We included data from the first and second Atlases, 1981-1985 and 2001-2005, respectively. Because the BBS and OBBA data are collected over different spatial scales, we summarized all data to a common resolution of 10 km^2 cells as per the OBBA data.

A suite of climate variables (Table 4.7) were selected a priori based on knowledge of biologically relevant factors important for determining distributions of Nearctic-Neotropical migratory birds over their breeding range and at the range margins (Venier *et al.*, 1999, Jiménez-Valverde *et al.*, 2011, Melles *et al.*, 2011). The climate variables were summarized over both annual and seasonal time periods reflecting the months associated with the breeding portion (May through August) of the annual cycle (Heikkinen *et al.*, 2006). Baseline climate data for the current time period (1950-2000) were retrieved from the Worldclim database, which is a set of high resolution interpolated climate data (Hijmans *et al.*, 2005), at a resolution of 10 km^2.

Projections of potential future climate suitability were based on four GCMs using the A2 emission scenario for the IPPC 4th Assessment, which depicts an intensive-fossil use future with moderate economic growth (Nakicenovic *et al.*, 2000). We selected the UKMO-HadCM3 (Hadley), CGCM2.0 (CCMA), CSIRO-MK3 (CSIRO), and NIES-99 (NIES) models, as they provide a range of variability with respect to annual temperature and cumulative precipitation predictions (IPCC, 2007a). Climate data from each GCM were downscaled using thin plate spline spatial interpolation of anomalies of original GCM outputs (Ramirez & Jarvis, 2008). Future projections of climate suitability were based on averages describing three thirty-year time periods defined as the 2020s, 2050s, and 2080s.

To better understand which climate variables were driving the differences in future projections of suitable habitat, following Garcia *et al.* (2011), we assessed the deviations among

GCMs during late century projections (2080s) as this is when inter-model variations within emission scenarios become most pronounced (Beaumont *et al.*, 2008). For each climate variable used in the SDM, we applied model performance metrics to distinguish between the variable for each individual GCM and the multi-model median ensemble for the same variable (Duan & Phillips, 2010). The signed standardized anomaly, *D*, is the spatially aggregated root mean square (*RMS*) difference between each individual GCM variable and the multi-model median ensemble for the same variable. *D* is standardized using the standard deviation of all GCMs. *D* reflects how much a GCM (for each variable) tends to over- or under-estimate the variable in relation to the median. *D* values close to zero indicate similarity with respect to the median. The spatial Pearson correlation (*R*) quantifies the similarities in spatial patterns between individual GCMs for a given variable and the median of that variable. Values range between -1 and 1, with values close to 1 indicating agreement among variables between GCMs.

4.3.3   Species distribution models

SDMs were developed using the maximum entropy model, MAXENT v. 3.3.3e (Phillips *et al.*, 2006, Phillips & Dudik, 2008). A geographic layer describing absence locations of BBS routes surveyed without evidence of the species and OBBA squares were used as background points. These were constrained to within a 300 km region outside of the minimum convex polygon surrounding all presence locations, reflecting regions that were accessible and of similar ecosystems to their current locations (Lobo *et al.*, 2010, Barbet-Massin *et al.*, 2012a). SDMs were developed using different combinations of variables evaluated and compared using the area under the curve (AUC) of the receiver operating characteristic (Fielding & Bell, 1997) based on 10-fold cross validation. All spatial data were projected using the Behrmann equal-area projection.

To address the influence of GCM selection on range distributions under future climate changes, the SDMs were projected forward using spatial data corresponding to the future conditions of the four GCMs across the 2020s, 2050s, and 2080s. We generated a climate-model consensus forecast based on the median of each variable for the three future time periods, which were then used to forecast the potential range shift of the Hooded Warbler into the 2020s, 2050s, and 2080s (Fordham *et al.*, 2011). This resulted in five SDM future projections that were used as suitability layer inputs to the metapopulation dynamics model.

4.3.4 Metapopulation demographic model

The Hooded Warbler metapopulation model comprised a two-stage stochastic matrix model for each population, which was linked to other populations through a dispersal distance function (Tischendorf, 2003). The metapopulation model was developed using demographic parameter estimates based on a combination of empirical knowledge derived from populations occurring within southern Ontario and expert knowledge through a series of workshops (Table S1 Supp Info) (Tischendorf, 2003). The model included juvenile and adult stage classes, where individuals were considered adults after 1 year based on a post-breeding census. Only adults have a non-zero fecundity rate and survival estimates were stage-specific. Demographic stochasticity was included via a Poisson distribution while environmental stochasticity was modeled by drawing each vital rate from a random variate drawn from a lognormal distribution using the mean and standard deviations of each vital rate.

Dispersal among populations was modeled as a negative exponential decay function in RAMAS GIS v. 5.0 (Akçakaya & Root, 2005) as

$$m_{ij} = a \times \exp(- D_{ij}^c / b)$$

where m_{ij} is the dispersal rate between the ith and jth populations, a (scaling parameter), b, and c are function parameters, and D_{ij} is the distance between the edge of two populations (Akçakaya & Root, 2005). Initial abundances for each patch occupied in 2000 were based on focal surveys undertaken for this species across the southern Ontario landscape during 1997, 1998, and 2000 and expert knowledge (Tischendorf, 2003).

4.3.5 Landscape scale dynamic suitability maps

We applied a two-stage hierarchical procedure to derive relative habitat suitability for the Hooded Warbler to reflect suitability occurring at the biogeographical and landscape scales (Pearson *et al.*, 2004). First, the current and future projections of relative climate suitability from the SDMs were used to identify suitable regions at the biogeographical scale. Secondly, we derived a binary suitability layer of forest cover at the landscape scale over southern Ontario (Fig. 4.8.2), which was used to define discrete patches of suitable habitat and the spatial structure of the metapopulation (Akçakaya & Root, 2005). Within southern Ontario, the Hooded Warbler

relies on mature mixed hardwood forest stands with gaps where early successional vegetation provides suitable nesting habitat during the breeding season. To capture these habitat dependencies, we reclassified a high resolution (15 m) land cover classification for southern Ontario (Ontario Ministry of Natural Resources, 2007) to a binary forest map. This spatial dataset was selected because its high resolution and land cover classes enabled the delineation of habitat patches that most closely reflects the known distribution of habitat patches on the ground. Furthermore, while other data sets have broader spatial coverage (e.g., GlobCover, GLC2000), disagreements in individual forest cover classes and their spatial distribution were cause for concern (Fritz *et al.*, 2011). Deciduous and mixed forest cover classes were reclassified to a binary suitability map where habitat suitability values ranged from 0 (low) to 1 (high). As an area sensitive species, it is rarely found breeding in habitat patches smaller than 1 km^2 (Flaxman, 2004), thus we excluded regions of forested cells less than 1 km^2.

The relative habitat suitability values based on the SDM outcomes were modified by multiplying it with the binary forest habitat map. This resulted in non-forested regions masked from the suitability layer. To determine the spatial structure of the metapopulation over time, the current and future relative habitat suitability maps were linearly interpolated to produce annual maps of suitability (Keith *et al.*, 2008, Anderson *et al.*, 2009). To delineate suitable and unsuitable regions across the range, we applied the 5th quantile of habitat suitability values as the threshold. The values were extracted across all known occurrence locations from the current SDM prediction layer. This threshold value minimized omission error and resulted in a higher commission error, which was expected given that the species is not in equilibrium with the environment at its expanding northern latitudinal range margin (Araújo & Pearson, 2005, Melles *et al.*, 2011).

RAMAS GIS was used to identify patches consisting of cells above the habitat suitability threshold for each annual map using a patch-identification algorithm described in Akçakaya & Root (2005). Adjacent cells of suitable habitat were considered part of the same habitat patch if they were within a 2 km distance of suitable habitat cells. RAMAS GIS simulates the dynamics of a metapopulation using a stochastic stage-structured model for each population. Habitat, and thus the number of populations, at any given time step is based on dynamic climate changes with forested habitats remaining constant over time.

The relative habitat suitability models and the demographic model are linked through the carrying capacity parameter for each habitat patch. Carrying capacity was considered a function of the total habitat suitability (*ths*) of each patch, a composite measure that considers both the size of the patch and the habitat suitability across all grid cells (Akçakaya & Root, 2005). Specifically, *Carrying capacity = ths* * 5.5, where 5.5 represents the average density per km^2 of breeding male Hooded Warblers. The average density was based on records of population census of one patch undertaken over a period of ten consecutive years between 1992 and 2002 (Badzinski, 2003). A ceiling model of density dependence was applied, such that when population sizes exceeded a ceiling threshold, the population size was reduced below the threshold. The ceiling thresholds were based on both the amount and suitability of habitat. We address the uncertainty associated with these estimates and other demographic parameters through a global sensitivity analyses.

4.3.6   Global sensitivity analyses and Simulations

Metapopulation dynamics were simulated assuming a static future climate, and potential future climate changes according to each of the four GCMs and one GCM consensus approach. The static scenario assumed that climate suitability remained unchanged from current conditions, such that species abundances and the range margin position were driven by the currently suitable habitats and demographic processes. In the climate change scenarios, occupancy patterns over space and time and predictions of species viability were driven by climate changes and demographic processes. For each scenario, metapopulation dynamics were simulated with 1000 replicates for 100 years (i.e. years 2000 – 2099). Patterns of projected future patch occupancy, change in total habitat suitability, and expected minimum abundances (EMA) across the 1000 replicates were compared among the different climate model treatments (McCarthy & Thompson, 2001).

To model the direct loss of habitat and its influence on predicted extinction risk, we simulated the removal of habitat patches. Habitat patches were randomly removed from the landscape and the number of patches (i.e. populations) removed for each replicate was randomly sampled from a uniform distribution with a minimum of 5 and the maximum number of patches equivalent to the number found within the static climate scenario. Our intent here was to develop

a null model of habitat loss as the assumption of static future habitat is unlikely, and not to develop realistic habitat loss dynamics.

We applied global sensitivity analyses (Saltelli *et al.*, 2006) to evaluate the influence of uncertainty in demographic parameters on measures of extinction risk. Mean parameter estimates were sampled from probability density functions allowing us to capture the full range of variability associated with the different estimates (Table 4.2). The probability density functions were selected based on knowledge of the species and were confirmed by experts (Badzinski, 2003, Tischendorf, 2003). The sensitivity analysis was implemented using a modified version of the program GRIP (Curtis & Naujokaitis-Lewis, 2008). A separate global sensitivity analysis was performed on the static climate scenario, and on each of the five climate scenarios both with and without habitat loss resulting in a total of 65,000 replicates (5,000 replicates per scenario).

To compare and rank the relative influence of the varied parameters, including the choice of GCM and direct habitat loss, on EMA, we used random forests (RF) prediction model (Breiman, 2001). The random forest method provides measures of variable importance for each predictor (Breiman, 2001, Liaw & Wiener, 2002) by calculating the percent increase in the mean square error (Liaw & Wiener, 2002).

4.4   Results

4.4.1   Distributions under current and future climate conditions

The model including all climate variables produced the highest AUC score (0.802), where an AUC value between 0.7-0.9 is considered a good model (Swets, 1988). At the biogeographical scale, the current breeding distribution of the Hooded Warbler is highly correlated with climate variables. Based on their contribution to increasing the regularized gain in the MaxEnt model, mean annual temperature seasonality, mean annual precipitation seasonality, and maximum breeding season temperature were the three most important variables (Table 4.7.1). Predicted relative habitat suitability appears spatially structured with relatively high values predicted across the latitudinal gradient of the range (Fig. 4.8.2). Some of the most suitable regions were predicted in southern Ontario, at its expanding range front.

Projections of potential future breeding distributions across the four GCMs and the consensus model suggest that future climate changes may result in range-wide shifts of relative suitable habitat (Fig. 4.8.2). By the 2080s, the breeding range is projected to shift northward and is characterized by loss of suitable habitats in the southern portion of the range and gains in regions north of its current range margin. However, the four GCMs used resulted in divergence among projections in terms of the magnitude of potential losses and gains of suitable habitat at the southern and northern range portions (Fig. 4.9.1). For example, predictions from the NIES GCM resulted in the largest loss of relatively suitable habitat by the 2080s over the entire range due to disproportionate losses in the southern portion of its current range and limited gains in suitability north of the current range margin. In contrast, predictions from the CSIRO GCM led to projections with the most gains north of the current range margin, and the fewest losses in the southern part of the current distribution. Projections derived from multi-model consensus of GCMs captured the central tendency of the GCMs.

Based on the *D*-statistic, the NIES and Hadley GCMs tended to diverge more from the median relative to the CCMA and CSIRO GCMs, and often in different directions (Table 4.7.3; Table 4.9.2, 4.9.3). In particular, there were relatively large differences in magnitude and direction of the temperature and precipitation seasonality variables, which were the most important variables in the MaxEnt model predictions (Table 4.7.2). Based on the *R*-statistic, there was generally a high degree of similarity among the four GCMs and the multi-model median consensus GCM for the majority of the climate variables (Table 4.7.3). Of all GCMs, the NIES GCM consistently had the lowest *R*-values across all variables, indicating the most divergence from the consensus. The largest deviations were evident for cumulative precipitation over the breeding season, especially for the NIES and Hadley GCMs.

4.4.2   Effect of future climate changes on species persistence

Under the static climate scenario, the metapopulation dynamics model predicted an increase in the average number of occupied populations over the 100 year time period (Fig 4.8.3). The predicted number of occupied populations increased from 39 to 60 populations. There was a large degree of variability in the projected occupancy trends depending on the GCM used (Fig 4.8.3). Both CCMA and CSIRO GCMs led to projected increases in the number of occupied populations over time and relative to the static climate scenario. The Hadley GCM led to

projected decreases in the number of occupied populations, with occupancy consistently lower than the static climate scenario. The NIES GCM produced non-monotonic behaviours in occupancy projections, with increases up until the 2050s and declines during the 2080s. The consensus GCM led to projected increases in occupied populations over time that were consistently higher than the static climate scenario.

Projections of occupied populations and metapopulation abundances did not consistently track changes in total habitat suitability (*ths*) at the landscape scale (Fig. 4.8.3). For example, the CCMA GCM resulted in projected declines in *ths* starting around 2080, while trends in occupied populations and abundances were clearly increasing. In other cases, such as the consensus GCM, the direction of trends was similar while the magnitude of changes in projected occupancy or abundance trends did not follow suit. Hadley and NIES GCMs were the only models where projected changes in total habitat suitability and occupied populations and metapopulation abundances were roughly concordant. Furthermore, the decoupling of trends between *ths* and projected occupancies and abundances was more apparent in time periods further into the future.

Based on EMA, the Hadley GCM led to greatest risks of decline relative to any other GCM (Table 4.7.4). Each individual GCM resulted in EMAs less than the static future climate scenario, whereas the consensus GCM had the largest EMA. Using change in *ths* as an index of risk, the largest risks were associated with NIES, Hadley, static, consensus GCM, CCMA, and CSIRO, in declining order.

4.4.3   Global sensitivity analyses

Under scenarios of dynamic future climatic conditions and no direct habitat loss, the most influential parameters on EMA based on their propensity to lead to increases in the overall mean square error included juvenile survival, adult survival, adult fecundity, mean dispersal rate, and the number of connections (Fig. 4.8.4). Variability associated with the choice of GCMs was ranked sixth out of 14 variables, followed by the total number of populations in the entire metapopulation. In contrast, simulations where climate change and direct habitat loss were explicitly varied revealed the importance of habitat loss as a contributor to EMA as it was ranked fourth most important, behind adult survival, juvenile survival, and adult fecundity (Fig 4.8.4).

Variability with the choice of GCMs moderately influenced EMA based on its contributions to the percent increase in mean square error (ranked 8th out of 14 variables).

4.5   Discussion

By using coupled SDM metapopulation dynamics models, we illustrate how a combination of changes in suitable habitats, demographic processes, and stochastic processes influenced predictions of species persistence at the northern range boundary. The ranking of uncertainties through the PVA framework and global sensitivity analyses showed how variability in the choice of GCMs propagated through the coupled models and projections over multiple spatial scales.

Our results clearly show how variability in choice of GCMs affects the SDM projections and propagates through to metapopulation viability projections at the northern range boundary. In some cases, opposite trends in viability metrics were evident, especially for the more extreme climate projections such as the Hadley and NIES GCMs. Comparing viability estimates and metapopulation dynamics across different GCMs demonstrates the potential bias should metapopulation projections be based on any single GCM. While both distribution and metapopulation viability projections highlighted the different trends as a function of the GCM applied, further interrogation of the climate variables used in the SDM revealed the variables driving the differences among projections. In particular, we recommend the *D*-statistic (Duan & Phillips, 2010, Garcia *et al.*, 2011) as a diagnostic alongside the ranking of important predictors in the MaxEnt model to better understand variables driving differences among projections.

The degree of concordance among landscape level measures of habitat suitability (*ths*) and metapopulation viability metrics was sensitive to the choice of the GCM. While the more extreme GCMs resulted in more consistency between the habitat-based and viability metrics, the differences were more amplified during late-century projections. The lack of tracking in *ths* by metapopulation dynamics (Fig. 4.8.3) points to limitations of using changes in habitat suitability measures on their own as proxies for extinction risk when assessing potential future climate change impacts (Fordham *et al.*, 2012a). Our measures of extinction risk were a function of metapopulation dynamics models that incorporate demographic and dispersal processes, which are likely key to understanding species vulnerability to climate changes, especially in patchy and dynamic landscapes.

For species inhabiting heterogeneous and patchy landscapes at range boundaries, the use of process-based demographic models provide additional insights into dynamics and factors limiting range shifts not captured by SDMs that are undertaken at the biogeographic scale. The integration of simulated direct losses of habitat in conjunction with potential future climate changes strongly influenced EMA. These findings suggest that although future climate changes are likely to contribute to range margin expansions at the northern latitudinal boundary for the Hooded Warbler, the ability to track such changes is dependent in part on the availability of suitable biotic habitat elements. This corroborates findings across both empirical and theoretical studies (Warren *et al.*, 2001, Travis, 2003, Wilson *et al.*, 2010). Although simulated direct habitat losses were randomly removed from the landscape without consideration of their size or relative position, we applied this as a null model, and future work is focused on the development of more realistic loss scenarios. However, we expect that the null model applied here will result in more conservative risk estimates. Despite the assumption of random habitat loss and uncertainty of various demographic parameters, our results emphasize the importance of managing to retain currently suitable patches at the range margins (Hodgson *et al.*, 2011).

Consensus approaches are used as a method to deal with uncertainty in climate models with the goal to reduce the overall variability among predictions (Knutti *et al.*, 2010). Projections based on individual GCMs enabled exploration of the range of potential outcomes, and importantly highlighted extremes. This was especially evident at the scale of the metapopulation dynamics model where predicted occupancies and abundances were sensitive to the choice of GCM resulting in trends occurring in opposite directions (i.e. increases versus decreases in predicted metapopulation occupancy). In particular the Hadley and NIES GCMs projected more extreme range contractions by the 2080s, and subsequently influenced risk estimates of the metapopulation dynamics model. Despite the central tendency consensus GCM, it had the highest EMA leading to interpretations of lowest risk relative to other future climate scenarios explored. Overall, the use of consensus climate models will depend on the research question, management problem, and behaviours regarding risk aversion. Here, we were interested in understanding the implication of variability of GCMs on risk estimates derived from metapopulation dynamics models, thus justifying an exploration of the range of possible conditions. This method also allowed for the ranking of uncertainty associated with GCMs, direct habitat loss, and demographic parameters, which is useful for prioritizing future research

and management actions. In cases where more GCMs are included, adopting clustering techniques to group similar GCMs may prove helpful and tractable (Garcia *et al.*, 2011).

Range margins are dynamic and reflect a complex set of interacting factors including suitability of climate conditions, presence of suitable habitats, and biotic interactions, all of which interact with demographic processes (Caughley *et al.*, 1988, Lawton, 1993). Based on the global sensitivity analyses, uncertainty in vital rates strongly influenced EMA risk estimates, likely a reflection of environmental fluctuations faced by range edge populations and uncertainty in their estimates. Although this suggests a need to prioritize data collection to refine these estimates in the short-term, direct habitat losses were also ranked highly suggesting the need to prioritize habitat protection within this landscape. While we did not explicitly examine the timing of habitat prioritization, this region was consistently projected to remain suitable habitat across all time periods and GCMs.

Threats are dynamic and may operate over multiple scales, reinforcing the need for risk assessments and the implementation of management actions across different planning levels. This is especially true for wide-ranging species where quantifying potential risks from climate changes and habitat loss may require a two-stage SDM that captures broad-scale climate influences with fine-scale habitat preferences (Pearson *et al.*, 2004). Furthermore, species found in patchy landscapes may necessitate the use of finer-scale habitat data derived from regional efforts, which may increase the relevancy of outcomes to management jurisdictions (Bradbury *et al.*, 2011).While SDM future projections identified a region of high suitability within southern Ontario robust to the choice GCMs (Fig. 4.9.2), the design of conservation strategies would ideally integrate outcomes of the metapopulation dynamics model. In particular, the dynamics models and simulated direct habitat losses highlight how finer-scale habitat features may become limiting in the future. Further evaluation of the effect of alternative management actions, and their costs effectiveness on species viability (Wintle *et al.*, 2011, van Teeffelen *et al.*, 2012) under potential future climate changes would complement our analyses. A decision-theoretic approach would be particularly useful to assist with decisions regarding the timing of alternative management actions when climate changes result in temporally and spatially variable landscapes (Wilson *et al.*, 2007).

4.6   Acknowledgements

4.7   Tables

Table 4.7.1 Species distribution model predictor data descriptions, abbreviations, and percent contribution of predictors to MaxEnt species distribution model gain for the Hooded Warbler breeding distribution. Model gain is the average log probability of the presence samples minus a constant.

Variable	Description	Abbreviation	Percent contribution
Annual temperature seasonality	Standard deviation *100 of annual temperature	Tseas	52.5
Annual precipitation seasonality	Coefficient of variation of annual precipitation	Pseas	29.3
Maximum spring and summer temperature	Mean of the monthly maximum temperature calculated between April-August	Tmaxbr	6.5
Mean annual temperature		Tann	6
Cumulative spring and summer precipitation	Cumulative precipitation over April-August	Pbr	3.4
Mean temperature coldest quarter		Tcoldq	2.3

Table 4.7.2 Demographic parameters varied in the global sensitivity analyses: estimates used in the PVA model, probability density functions (PDFs) applied and range of parameter uncertainty.

Parameter	Mean estimate	PDF and range of values
Juvenile survival rate	0.32	Lognormal distribution, mean = 0.32, SD = 0.064[1]
Adult survival rate	0.64	Lognormal distribution, mean = 0.64, SD = 0.128[1]
Juvenile fecundity	0	Not varied
Adult fecundity	1.404	Lognormal distribution, mean = 1.404, SD = 0.064[1]
Initial abundances	200	Normal distribution, mean = 200, SD = 40
Carrying capacity	Function of total habitat suitability per habitat patch and average territory size	Varied based on relative habitat suitability derived from SDMs based on four General Circulation Models, and two ensemble methods (SDM and GCM)
Model of density-dependence	Ceiling to carrying capacity	Not varied
Rmax	1.02	Normal distribution, mean = 1.02, SD= 0.102
Correlations among vital rates	No correlation	Uniform distribution (minimum = 0, maximum = 1)
Dispersal rate	Negative exponential function of the form: $m_{ij} = a \times exp(-D^c_{ij}/b)$	Normal distribution, mean = 0 and SD =0.1. This modifies the dispersal rate between populations i and j, where the new dispersal rate $m'_{ij} = m_{ij} + m_{ij}n$
Maximum dispersal distance	120 km	Normal distribution, mean = 120, coefficient of variation = 20%

Parameter	Mean estimate	PDF and range of values
Number of habitat patches (i.e. populations) at time = 0	88	Uniform distribution, minimum = 5, maximum = 174

[1]Tischendorf (2003)

Table 4.7.3 Performance metrics *D* and *R*. *D* is the spatially aggregated root mean square (*RMS*) difference between each individual GCM variable and the multi-model median ensemble for the same variable for the 2080s forecasts. *D* is standardized using the standard deviation of all GCMs. *D* reflects how much a GCM (for each variable) tends to over- or under-estimate the variable in relation to the median. *D* values close to zero indicate similarity with respect to the median. The Pearson correlation (*R*) quantifies the similarities in spatial patterns between individual GCMs for a given variable and the median of that variable.

		Climate variables					
		Tann	Tcoldq	Pseas	Tseas	Pbr	Tmaxbr
D-statistic	CCMA	-0.093	-0.059	0.043	-0.068	-0.135	-0.120
	CSIRO	0.058	0.054	-0.130	-0.191	-0.056	-0.046
	Hadley	-0.126	-0.244	-0.111	0.471	0.093	-0.046
	NIES	0.412	0.354	0.298	-0.282	0.364	0.328
R-statistic	CCMA	0.997	0.998	0.944	0.981	0.950	0.995
	CSIRO	0.998	0.997	0.934	0.986	0.920	0.995
	Hadley	0.998	0.996	0.948	0.977	0.887	0.998
	NIES	0.992	0.981	0.827	0.845	0.651	0.986

Table 4.7.4 Expected minimum abundance predictions for the static future climate, four GCMs, and consensus GCM scenarios

Experiment	EMA
Static	203
CCMA	197
CSIRO	199
Hadley	10
NIES	156
Ensemble	251

4.8 Figures
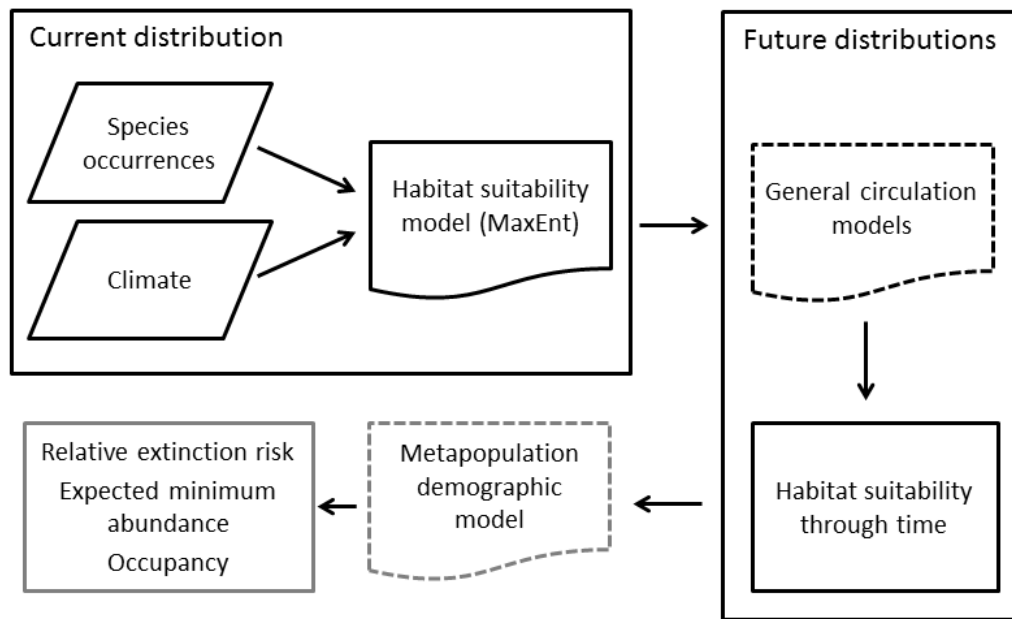
Figure 4.8.1 Hierarchical modelling framework of the coupled SDM-PVA analysis. Hatched boxes reflect the sources of uncertainties targeted in this study, which include the choice of GCMs, demographic parameter uncertainty, and direct habitat loss. Black boxes reflect models applied at the scale of the entire breeding range and grey boxes reflect models applied at the landscape scale.
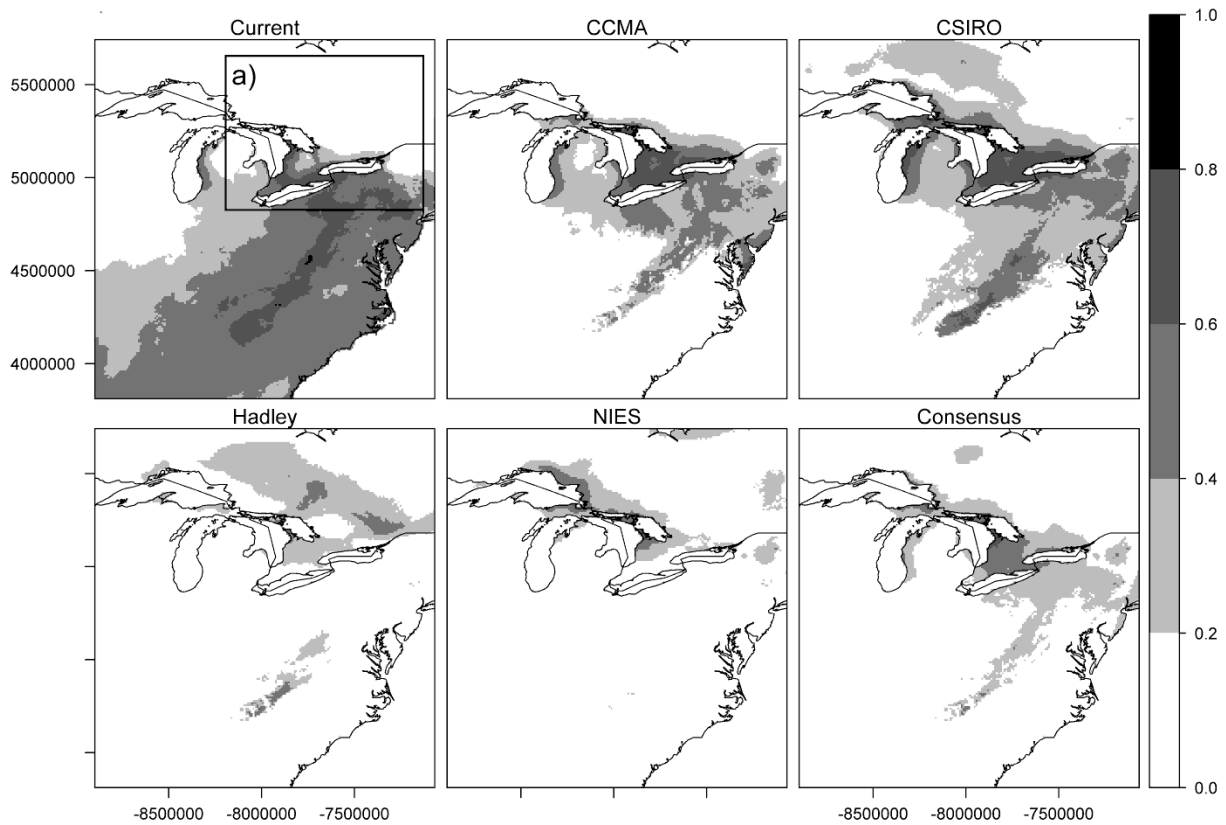
Figure 4.8.2 Predicted current habitat suitability across the entire breeding range (Current) and projections of potential future habitat suitability for the Hooded Warbler for 2080s for four GCMs and the consensus GCM. Inset (a) of the current predictions delimits the spatial extent of the landscape scale metapopulation dynamics model.
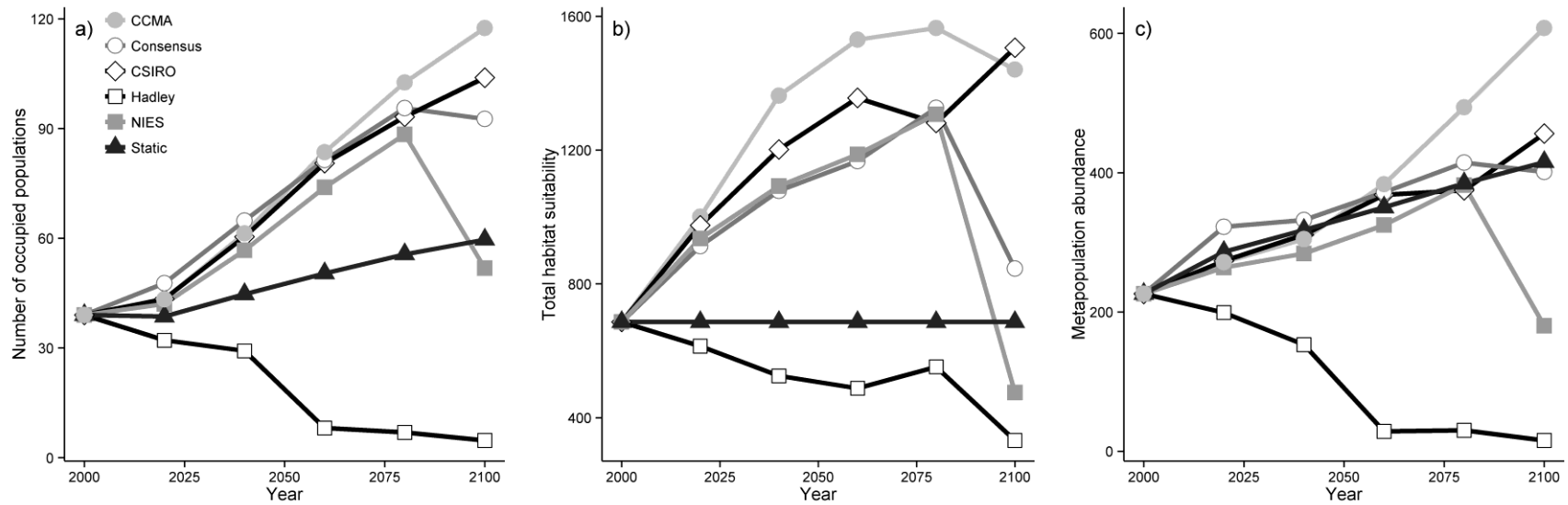
Figure 3. Predicted change in (a) average metapopulation occupancy, (b) total habitat suitability, and average metapopulation abundance over time for the static future climate scenario, four GCMs, and the consensus GCM.
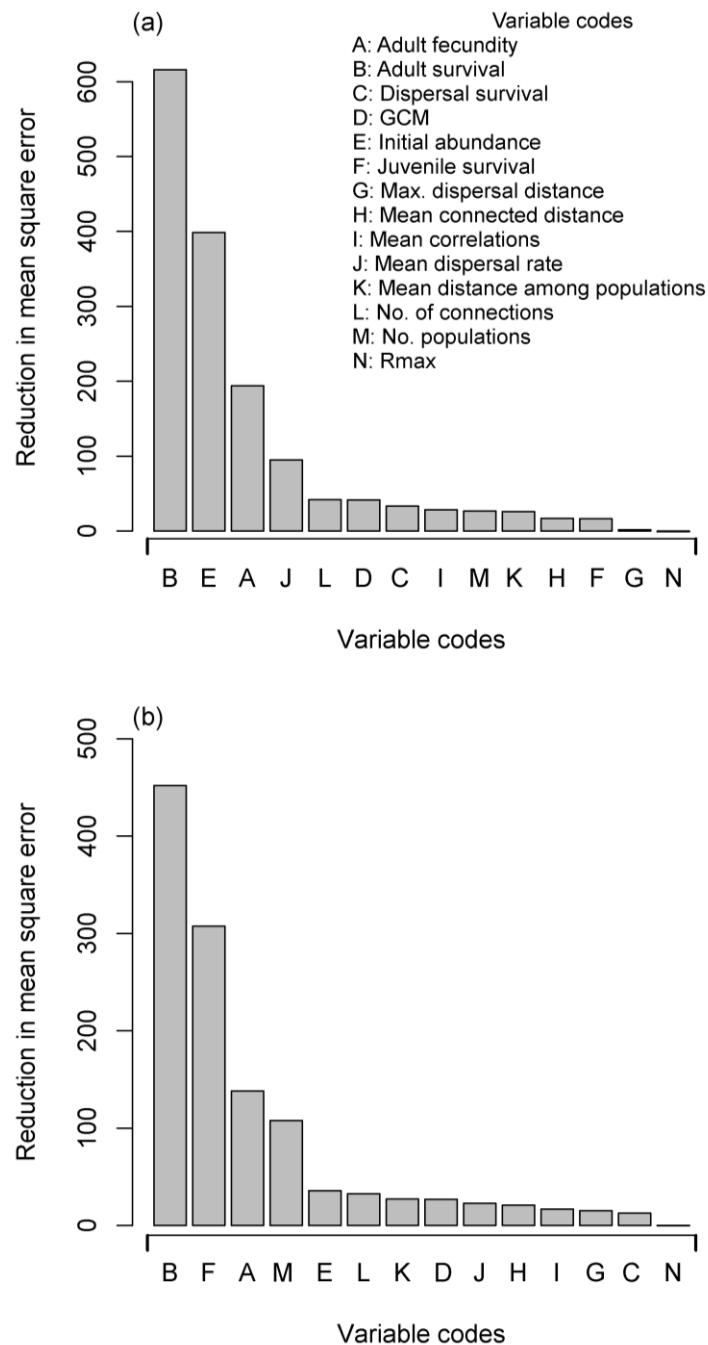
Figure 4.8.3 The relative influence of (a) choice of GCMs and demographic parameter uncertainty and (b) choice of GCMs, demographic parameter uncertainty, and direct habitat loss on expected minimum abundance based on the Random Forest variable importance metric of reduction in mean square error (MSE)

4.9 Appendix

4.9.1 Tables

Table 4.9.1 Life history characteristics used to inform parameterization of the metapopulation demographic dynamics model. ON: Ontario, PA: Pennsylvania. Table sourced with permission from (Tischendorf, 2003).

Characteristic	Observation	References
Breeding period (ON)	mid-May to late July	(Bisson & Stutchbury, 2000)
Clutch size	3.5	(Bisson & Stutchbury, 2000)
Broods/year (PA)	1.2 (possibly lower in ON)	(Evans Ogden & Stutchbury, 1996)
Incubation period	12 days	(Ogden & Stutchbury, 1994)
Fledging period	28 days	(Ogden & Stutchbury, 1994)
Maturity	breed at 1 year	
Life Span	8 years maximum, 2.5 years estimated average	(Ogden & Stutchbury, 1994)
Nesting Success	82% of nests fledged (ON: 1998)	(Bisson & Stutchbury, 2000)
Fledging Success	2.6 $\pm$ 0.29 fldg (n = 22) (ON: 1998)	(Bisson & Stutchbury, 2000)
Ontario Population Size	251 males / 225 females	Badzinski, pers. comm.
Annual Survival	juvenile 0.32 ± 0.064; adult 0.64 ± 0.128	Badzinski, Friesen, pers. comm.
Return Rate to Study Site (PA)	52% for males (n = 174) 43% for females (n = 195)	(Howlett & Stutchbury, 2003)
Dispersal/Movement	Average 10-20 km; max. 120 km	Badzinski, Friesen, pers. comm.
Average Territory Size	Average 7.2; minimum 1.6; maximum 8.5	Badzinski, pers. comm. Howlett and Stutchbury 1997
Habitat Requirements	Small clearings in the interior of large mature hardwood forests, well closed canopy	(Sedgwick & Knopf, 1987, Donovan & Flather, 2002, Shifley *et al.*, 2006)
Sex Ratio (ON: 1998)	83% of males paired 40 – 45 % females in population	(Bisson & Stutchbury, 2000) Badzinski, Friesen, pers. comm.
Trend in Population Size	steady increase since from	Badzinski, unpubl. data

Characteristic	Observation	References
	(80-176) in 1988 to 251 in 2002	

Table 4.9.2 Current and projected future climate variables over three future time periods, 2020s, 2050s, 2080s, derived from four general circulation models (GCMs) over Eastern North America. Future climate variables are based on annual averages or seasonal averages calculated over the breeding season of the Hooded Warbler (April through August).

		CCMA2			Hadley			NIES-99			CSIRO-MK3		
	Current	2020	2050	2080	2020	2050	2080	2020	2050	2080	2020	2050	2080
Tann	66.2	84.5	98.8	120.1	78.9	94.2	117.7	85.0	117.2	157.1	85.9	103.0	131.1
Tmincoldq	-72.7	-50.8	-32.8	-9.7	-67.0	-48.9	-26.8	-55.6	-21.4	28.7	-51.4	-30.8	0.9
Pann	887.3	861.2	866.0	846.3	914.7	924.0	939.8	921.2	915.9	929.8	881.6	892.6	883.6
Pseas	31.9	33.7	33.3	33.6	32.4	32.1	31.5	32.0	32.8	37.1	32.1	31.1	31.2
Tseas	10282.3	10195.4	10050.2	9962.4	10750.0	10842.4	10934.2	10336.8	9959.6	9576.5	10117.6	10036.6	9741.1
Pbr	516.5	494.9	498.8	485.2	535.0	521.8	513.6	540.7	544.0	547.4	510.2	509.7	495.0
Tmaxbr	212.7	233.1	246.0	268.9	230.3	247.4	274.1	232.8	263.4	300.9	233.2	248.8	274.2
Tmeanbr	152.1	171.0	184.5	205.3	168.9	184.5	209.2	172.1	201.2	237.6	172.0	188.8	215.5
Tminbr	92.2	109.4	123.4	142.3	107.9	122.1	144.7	110.9	138.6	173.8	111.2	129.3	157.2

Table 4.9.3 Current and projected future climate variables over three future time periods, 2020s, 2050s, 2080s, derived from four general circulation models (GCMs) for the province of Ontario. Future climate variables are based on annual averages or seasonal averages calculated over the breeding season of the Hooded Warbler (April through August).

| | | CCMA2 | | | Hadley | | | NIES-99 | | | CSIRO-MK3 | | |
	Current	2020	2050	2080	2020	2050	2080	2020	2050	2080	2020	2050	2080
Tann	2.9	20.8	36.8	56.3	15.2	29.2	52.9	24.5	63.6	107.9	25.3	45.0	78.1
Tmincoldq	-165.2	-140.6	-118.4	-93.3	-158.4	-139.2	-114.4	-143.4	-93.1	-26.5	-141.8	-118.7	-81.1
Pann	725.8	736.5	721.9	755.8	774.7	792.4	813.1	762.7	808.5	858.4	732.7	755.7	758.3
Pseas	34.0	34.4	32.7	32.7	33.6	33.0	29.0	31.5	28.7	30.3	29.5	29.0	24.8
Tseas	12342.6	12184.9	11969.1	11822.9	12738.5	12678.3	12723.2	12206.2	11049.5	9933.1	12151.7	12050.8	11645.1
Pbr	438.4	446.9	430.3	449.5	478.0	467.8	457.9	459.6	491.6	513.8	431.4	438.8	415.9
Tmaxbr	164.0	181.7	196.7	216.8	179.2	192.9	219.7	186.4	218.7	256.1	189.2	209.5	242.5
Tmeanbr	105.0	123.4	138.2	157.6	120.6	133.6	158.6	127.5	158.5	194.8	127.8	147.4	178.8
Tminbr	46.6	65.7	80.1	99.0	62.4	74.8	98.0	68.2	97.8	133.1	66.8	85.9	115.6

4.9.2   Figures
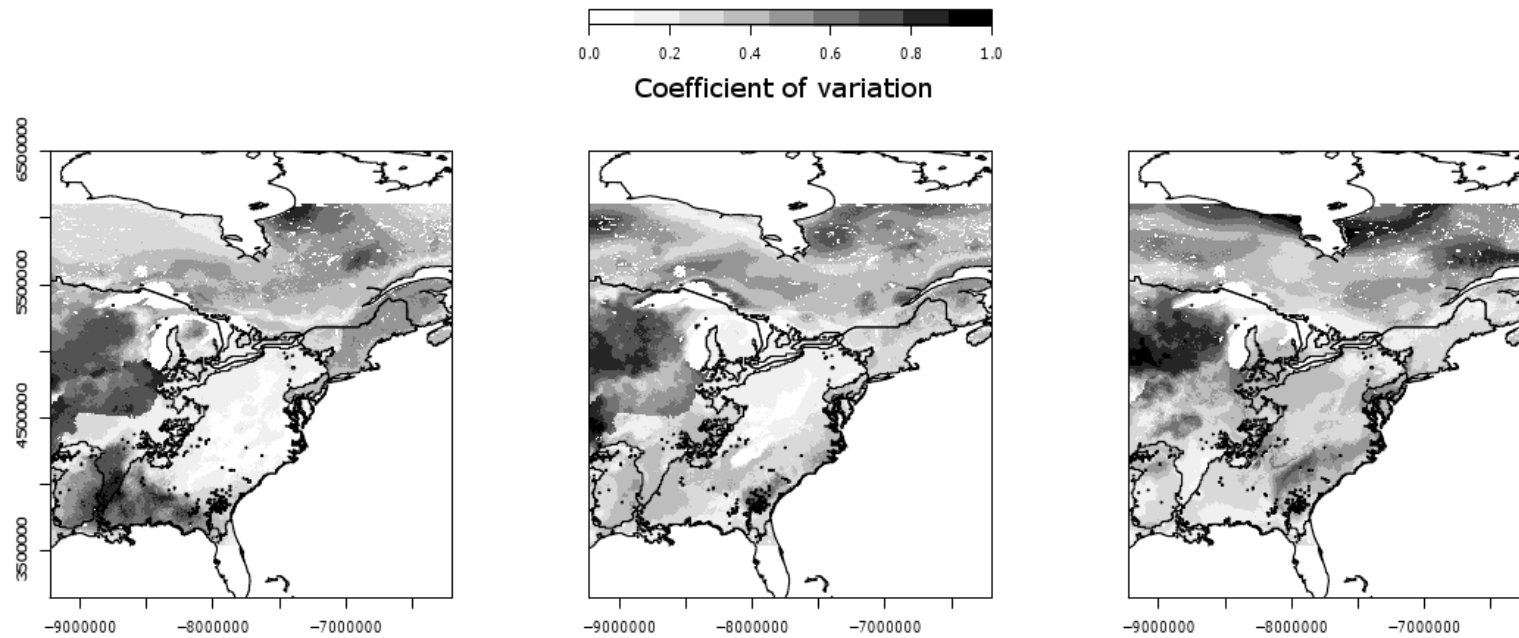
Figure 4.9.1 Uncertainty of Hooded Warbler relative suitability projections to the 2080s expressed as the coefficient of variation among four general circulation models: CCMA2, CSIRO, HADLEY, and NIES.
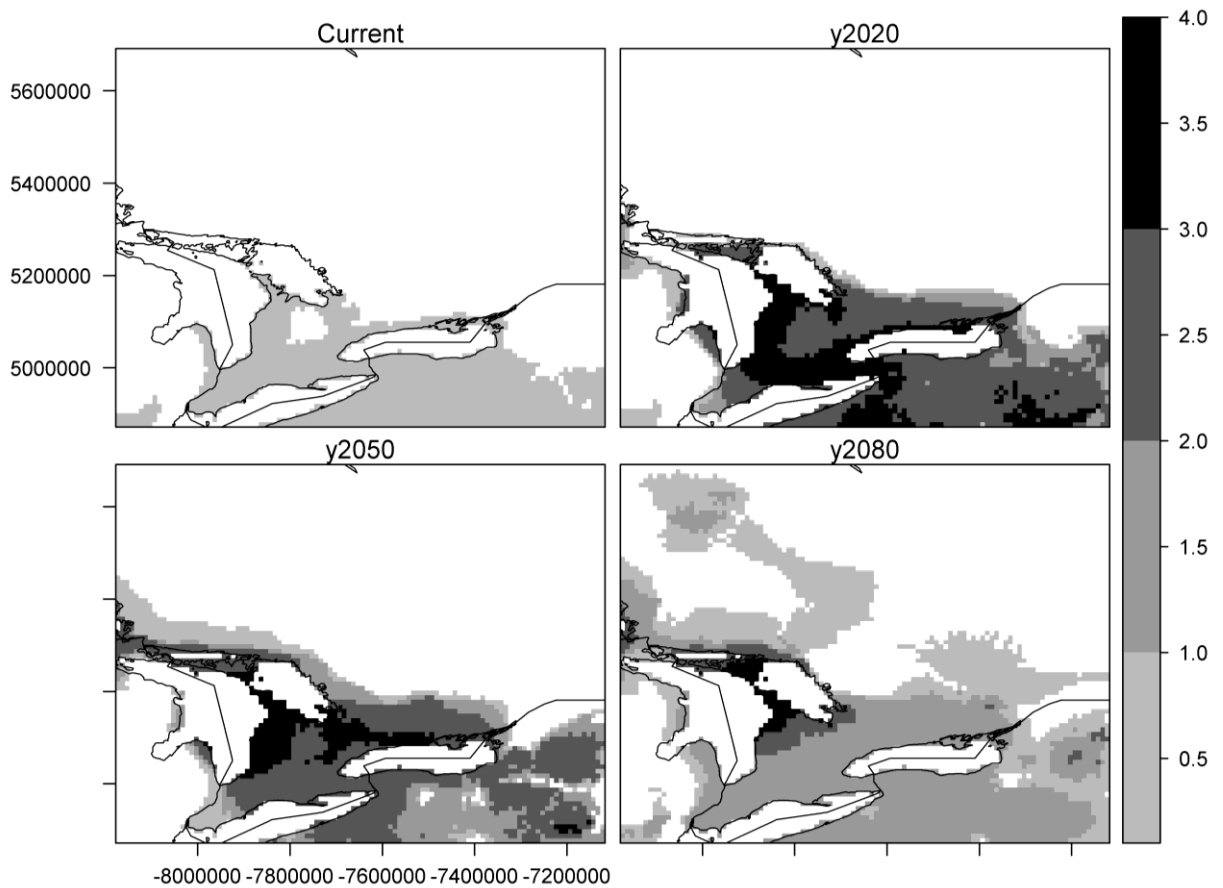
Figure 4.9.2 Overlap among Hooded Warbler binary presence/absence projections across the four GCMs for the 2020s, 2050s, and 2080s. Binary presence/absence maps were derived using the threshold for the current prediction model that corresponded to minimizing the absolute difference between the sensitivity and specificity (Liu *et al.*, 2005, Nenzén & Araújo, 2011). A value of four indicates complete agreement among all four GCMs, and 0, none

Chapter 5

5 Planning for Neo-tropical migratory bird conservation under climate change

5.1 Abstract

Migratory bird species present a unique challenge for conservation planning under climate change due to their complex life histories. Many species rely on disjunct breeding and nonbreeding habitats where regional variation in future climate across temperate and equatorial expanses may result in asymmetric range shift patterns. Despite the ecological significance of accounting for seasonal habitat dependencies, few studies characterize vulnerability to projected climate exposure across the annual cycle. As a result this factor is largely ignored when identifying spatial conservation priorities under climate change, limiting their potential utility. Furthermore, the range dynamics of vegetation dependent species will be constrained by a combination of climate change and habitat availability, yet biotic factors are rarely included in predictive models that are subsequently used as inputs to spatial priorities. While accounting for a range of model uncertainties, I quantified the sensitivity of spatial priorities under projected climate change to the inclusion of a habitat predictor variable within SDMs across breeding and nonbreeding ranges of 28 Nearctic-Neotropical migratory bird species. These results show that the addition of a single biotic predictor, forested habitats, had cascading influences on the selection of spatial priority areas for conservation. Identification of climatically suitable priority areas achieved lower representation of forested habitats required for vegetation dependent species relative to biotic derived priorities, in as a result of elevated commission error rates. Spatial incongruence between abiotic (climate) and biotic (forest) SDM derived priorities were amplified when projected climate change was considered while the pattern of spatial priorities varied in asymmetric ways depending on the seasonal range under consideration. High latitude breeding priorities resulted in large northward shifts, while differences in nonbreeding priorities were characterized by more

complex heterogeneous patterns. These results emphasize the importance of including ecologically relevant biotic predictors into SDMs especially when used as inputs to quantitative conservation planning assessments. Spatial conservation priorities have the potential to shift across national boundaries as species track suitable climates, further emphasizing the need for globally coherent collaborative actions to conserve wide-ranging migratory species.

5.2   Introduction

Recent climatic changes have resulted in large perturbations to biological systems including shifts in species distributions, population dynamics, ecological interactions, and species' phenology (Walther *et al.*, 2002, Parmesan & Yohe, 2003, Root *et al.*, 2003, Chen *et al.*, 2011a). Global climate change is therefore now considered a demonstrable threat to species and ecosystems requiring both mitigation and adaptation measures (Brook *et al.*, 2008). Protected areas are a cornerstone mitigation strategy of biodiversity conservation and are a key tool for climate change adaptation, yet their static nature brings into question their ability to address species range shifts in response to rapid climate change (Hannah *et al.*, 2002, Hannah *et al.*, 2007). Current protected areas have already undergone shifts in species representation due to recent changes in climate (Johnston *et al.*, 2013) and future projections of species range shifts suggest their capacity to buffer against future changes is unlikely (Araújo *et al.*, 2004, Hole *et al.*, 2009, Araújo *et al.*, 2011). Furthermore, suitable habitats for many species are likely to shift across political boundaries (Saura *et al.*, 2014). Thus global climatic changes have the potential to undermine protected area networks designed with national oriented conservation priorities (Moilanen *et al.*, 2013) and underscores the increasing importance of a globally coherent protected area network and transboundary collaboration (Hannah, 2010, Mazor *et al.*, 2013).

Migratory bird species present additional challenges for global priority setting and conservation planning under climate change as they require seasonal habitats separated by large distances and inhabit multiple political jurisdictions. By definition, migratory species, cyclically or periodically cross national borders, and thus require coordinated

protection during all phases of their annual lifecycle (2003). Given that these species inhabit disparate regions it is likely that over the course of their annual cycle they will be affected by changes in climate (Robinson *et al.*, 2008). Yet migratory birds may not be universally vulnerable to climate changes across their seasonal ranges due to asymmetry in spatial and temporal patterns of threat dynamics. For example, species found at higher latitudes are expected to undergo poleward range shifts due to relatively large expected changes in temperatures, while species inhabiting tropical regions may exhibit elevational shifts due to narrow anticipated changes in temperature and changes in precipitation regimes (La Sorte & Thompson, 2007, Sekercioglu *et al.*, 2008, Zuckerberg *et al.*, 2009, La Sorte & Jetz, 2010, Chen *et al.*, 2011c). Subsequently, design of protected areas will need to account for these different patterns of range shifts in migratory species whose seasonal ranges span both high latitude and equatorial regions to ensure robustness to climate changes. In addition to global variation in threats, the current configuration and coverage of protected areas is spatially biased across regions (Joppa & Pfaff, 2009, Schmitt *et al.*, 2009, Coad *et al.*, 2010), which may necessitate spatially varied and regionally derived expansion of current protected areas to achieve effectiveness both currently and when future climate changes are considered. Despite the strong biological underpinnings of a complete lifecycle approach, few macroecological studies (Somveille *et al.*, 2013) and climate-change vulnerability assessment frameworks address seasonal habitats required by migrants (Small-Lorenz *et al.*, 2013a). Failure to address the potential influence of climate change across all portions of the range may distort vulnerability assessments and evaluation of risks, resulting in ineffective conservation actions.

An increasingly common approach to assess potential exposure to future climate change, an element contributing to species' vulnerability (Williams *et al.*, 2008a), is through the use of species distribution models (SDMs) (Guisan & Thuiller, 2005). SDMs are correlative models that relate species occurrences to environmental variables. The spatial predictive outcomes can be used to inform systematic conservation planning processes (Margules & Pressey, 2000) that consider potential future climate change (Carvalho *et al.*, 2011, Kujala *et al.*, 2013, Lemes & Loyola, 2013). Their use in

conservation priority settings tacitly assumes that predictions adequately capture elements of species' distributions requiring conservation. When applied in the context of reserve design, SDMs are often formulated using abiotic variables (i.e. climate) to the exclusion of biotic factors and resource variables, including suitable vegetation habitats required by higher trophic level species (e.g., Hole *et al.*, 2009, Araújo *et al.*, 2011, Carvalho *et al.*, 2011, Johnston *et al.*, 2013, Kujala *et al.*, 2013, Lemes & Loyola, 2013); but see (Carroll *et al.*, 2010, Virkkala *et al.*, 2013, Cumming *et al.*, 2014, Scott *et al.*, 2014). Generally, abiotic factors, such as dimensions of climate, have been assumed to play a large role in species distributions at broad spatial scales (i.e. regional, continental, global) while biotic factors have commonly been regarded as important at smaller scales (Pearson & Dawson, 2003). Yet increasingly, evidence supports the role of biotic factors on species distributions at regional, continental, and global scales, emphasizing the need to consider these factors alongside climate (Wisz *et al.*, 2013). Given that many animal species are constrained by the spatial distribution of their biotic habitat resources in addition to the abiotic climate conditions that describe their physiological tolerances (Pelini *et al.*, 2009, Kissling *et al.*, 2010, Wisz *et al.*, 2013), both types of factors mediate species range dynamics, and may vary globally in spatially structured ways.

Inclusion of biotic factors for animal species tends to improve model predictions suggesting that these factors contain important non-redundant information, perhaps as they approximate resource requirements (e.g., Venier *et al.*, 2004, Araújo & Luoto, 2007, Heikkinen *et al.*, 2007, Meier *et al.*, 2010, Forcey *et al.*, 2011, Barbet-Massin *et al.*, 2012b, González-Salazar *et al.*, 2013) but see Triviño *et al.* (2011). Integrating biotic predictors into SDMs that represent resource dependencies, and the subsequent priorities they inform, is likely to increase the ecological realism of outputs as they link more directly to factors influencing population dynamics (Araújo & Luoto, 2007). Evidence for the role of biotic factors at broad-scale species distributions combined with generally increased predictive performance suggests that selection of appropriate predictors for SDMs is of ecological significance with practical relevance to spatial conservation prioritization. In the context of conservation planning, SDMs have received a relatively comprehensive treatment of uncertainty, including assessment of the influence of spatial

resolution, thresholds to convert to probabilistic predictions to binary (presence-absence) outcomes, model algorithm, spatial bias of presence/absence data, and climate change models (Wilson *et al.*, 2005, Carvalho *et al.*, 2010, Nenzén & Araújo, 2011, Arponen *et al.*, 2012, Kujala *et al.*, 2013). However, there has been little work that explicitly examines spatial variability in priorities resulting from the choice of alternative predictor variable sets, in particular those that include biotic elements.

Given that population-limiting processes occur over the combination of seasonal habitats for long-distance migratory birds (Holmes, 2007), I contrast spatial conservation priorities across both breeding and nonbreeding seasonal ranges under the consideration of climate change targeting three themes. First, I address the sensitivity of conservation priorities to the use of alternative predictive inputs based on SDMs developed using only abiotic predictors or a combination of abiotic and biotic (habitat-based) predictor variables. I consider the selection of predictor variables as an opportunity to integrate ecological theory into SDM development moving it beyond an issue solely of practical relevance (Austin, 2007). Second, I examine the spatial dynamics of conservation priorities under potential future climate change while accounting for uncertainties in predictive model algorithms, climate models, and dispersal estimates. I illustrate how spatial divergence among solutions is amplified between abiotic and biotic models under climate change. Finally, I evaluate the performance of current protected areas to protect biodiversity under projected climate change. Overall these results emphasize the importance of including biotic factors in SDMs across seasonal ranges as they capture resources directly related to species persistence, thus leading to more robust conservation priorities. This work contributes both methodological and conceptual advances to the fields of conservation planning and modeling of range dynamics under climate change.

5.3   Methods

5.3.1   Species distribution models

I modeled the distributions for 28 *Parulidae* species considered Nearctic-Neotropical migratory species with broad forest habitat associations for each species across both their breeding and nonbreeding ranges (Berlanga *et al.*, 2010)(Table 2.8.1). Both present and

future predictions were based on ensemble methods that derived a mean prediction based on outcomes from Chapter 2, where each species' seasonal range was modeled separately (see Appendices). I developed two sets of models for each species, (1) climate-only predictors (abiotic model class), and (2) climate-habitat predictors (biotic model class). The climate variables represent a combination of extreme and seasonal values of temperature and precipitation that are known to influence bird species distributions (Huntley *et al.*, 2008). They included temperature seasonality, precipitation seasonality, mean of monthly maximum temperature, and mean of monthly total precipitation. Maximum temperature and total precipitation were averaged over seasonal time periods reflecting the months associated with the breeding (April-July) and non-breeding (November-February) periods of the annual cycle (Heikkinen *et al.*, 2006). Baseline climate data for the current time period (1950-2000) were sourced from the Worldclim database, which is a set of high resolution interpolated climate data (Hijmans *et al.*, 2005), standardized to a 20 x 20 km resolution.

Biotic SDMs were developed using all abiotic predictors as well as percent forest cover and percent shrub-grass cover as biotic predictors. Percent forest cover for each 200 km^2 was derived by reclassifying forest categories from the GlobCover dataset version 2.3, a global land cover model that has an original resolution of 300 m, which provided a consistent land-cover classification method across the entire western hemisphere (European Space Agency, 2008). GlobCover consists of 22 global land cover types and I derived a composite forest class consisting of 9 of the original classes that contained a minimum of 15% forest cover representing coniferous, deciduous and mixed forest types. Percent shrub-grass cover was calculated for each 20 km grid cell by reclassifying four of the original classes consisting of a minimum 15% shrub cover. To capture variability associated with different atmosphere ocean global circulation models (AOGCMs) (Fordham *et al.*, 2011), projections of potential future climate suitability were based on four GCMs using the A2 emission scenario from the IPPC 4th Assessment. I selected the HadCM3, CCMA-CGM3, CSIRO-3K, and NIES-99 models, as they provide a range of variability with respect to annual temperature and cumulative precipitation predictions (IPCC, 2007a). Future climate surfaces were based on averages

describing thirty-year time periods defined as the 2080s (2060-2099), accessed from the International Centre for Tropical Agriculture (http://www.ccafs-climate.org/).

SDMs were developed using an ensemble-modeling approach to capture variability associated with different modeling algorithms (Araújo & New, 2007a). I used five different modeling algorithms implemented in biomod2 R package (Thuiller *et al.*, 2012) using R version 2.15.2 (R Core Team, 2013). This included two regression methods (generalized linear models and generalized additive models), and three machine-learning methods (Random Forests, generalized boosted regressions and MaxEnt). To evaluate the predictive performance of each model for each species across each seasonal range, I used a five-fold cross-validated random subset of 70% of the data to calibrate the model and the remaining 30% for model testing. Models were evaluated based on two discrimination capacity statistics, the true skill statistic (TSS) and the area under the receiver operating characteristic curve (AUC), on the cross-validated data, and calibration plots were constructed and evaluated (Jiménez-Valverde *et al.*, 2013). TSS was only used on the breeding models, which consisted of presence-absence models. Model projections were based on the final model run using 100% of the data (Araújo *et al.*, 2005) and were undertaken over the entire western hemisphere for the current period and the 2080s. For each species, I obtained 20 current modeled distributions (5 SDMs × 2 seasons × 2 model classes, abiotic and biotic), and 80 future projections of suitability (5 SDMs × 2 seasons × 2 model classes × 4 GCMs). I assumed percent forest cover would remain constant over time, while climate was dynamic.

5.3.2 Conservation prioritization

I estimated the differences in spatial dynamics of the priority areas between the seasonal ranges across potential future climate changes, and assessed the influence of integrating biotic features within SDMs, whose predictions formed the input to the identification of priorities. Below I describe (1) an overview of the Zonation software, (2) Zonation specifications for the baseline scenario that considers both current and future priorities under potential climate changes, (3) the methods applied to account for uncertainty across

SDM algorithms and AOGCMs, (4) the experiments devised to test the sensitivity of inclusion of habitat features, and (5) the comparative and statistical analyses.

I used Zonation v. 3.1 conservation prioritization framework and software to identify global-scale conservation priorities across seasonal ranges under potential future climate change (Moilanen *et al.*, 2005, Moilanen *et al.*, 2012). Zonation uses a reverse stepwise heuristic and iteratively removes cells from a landscape in an order that minimizes the marginal loss value. From a mathematical perspective, marginal loss (δ_i) is calculated as:

$$\delta_i = \max_j \frac{q_{ij} w_j}{Q_j(S) c_i},$$

where w_j is the weight of species j, q_{ij} is the fraction of the original full distribution of species j in cell i (i.e. level of representation), Q_j (S) is the fraction of the original distribution of species j in the remaining set of cells, S, c_i is the cost of adding site i. The outcomes are deterministic and expressed as a nested hierarchy of solutions across a landscape where, for example, the top 1% of areas selected as priorities is nested within the top 10% priority areas, and thus differs substantially from other prioritization approaches where species targets are set *a priori*. Additionally, it is possible to derive the proportion of a species' original distribution captured in the priority solutions over different levels of landscape retention. I applied the core-area Zonation analysis variant as it retains areas of high habitat quality (i.e. high probability of occurrence) for a species at a given location, even if it is depauperate of other species (Moilanen *et al.*, 2011).

To evaluate the shifting dynamics of priorities over time as a function of potential climate changes for each seasonal range, spatial priorities were assessed across a suite of analysis periods. Using the predicted outcomes of the SDMs for each species for the current and future periods as primary inputs to Zonation, I prioritized landscapes separately for the following periods: (1) current (2000), (2) future (2080), and (3) current and future combined (herein 2000 - 2080). The latter prioritization effectively includes four distributions prioritized simultaneously: (1) current, (2) future, (3) dispersal pathways i.e. connectivity from the current to the future, and (4) stepping stones i.e.

connectivity from the future to the current. Within Zonation, spatial connectivity between two time periods was implemented as a species interaction (Type 1) where the spatial distribution of a conservation feature is modified as a function of distance to a second distribution (Rayfield *et al.*, 2009, Carroll *et al.*, 2010). This transformation is based on a species-specific dispersal kernel such that overlapping high quality cells from both distributions are selected preferentially. Based on a literature review and lack of species-specific annual dispersal estimates, the scale of connectivity for all species was set to a distance of 20 km/per year to represent both natal and breeding dispersal behaviours, which is likely a conservative estimate for such highly mobile species (Tittler *et al.*, 2009, Chen *et al.*, 2011a).

Given the known variability associated with SDM algorithms and climate change models (Elith & Graham, 2009), I explicitly accounted for these sources of uncertainty by applying the info-gap theory technique of distribution discounting (Moilanen *et al.*, 2006). For each species and for each seasonal range, I derived an ensemble model of current predictions of relative habitat suitability based on the mean across each of the five SDM algorithms. A discounted distribution grid was created by subtracting 1 standard deviation (SD) from the mean of the predictions across the 5 SDM algorithms. The same procedure was applied across the mean of the future projections across each SDM algorithm, for each GCM separately. To account for the variability across GCMs, I applied a secondary discounting procedure. For each species, for each seasonal range), I derived a mean ensemble grid across the four GCM projections (already discounted to consider type of SDM variability), which was subsequently discounted by 1 standard deviation. This method uses SDM predictive suitability outcomes without applying a threshold to transform to presence-absences, thus incorporating uncertainty directly (Moilanen *et al.*, 2005). Each of these discounted distributions for 28 species, 2 seasonal ranges, and 2 time periods formed the inputs for the baseline and experiment prioritizations. All biodiversity features were weighted equally, but results were summarized based on representation across species grouped by degree of vulnerability (see below).

5.3.3   Replacement cost analyses

Design of protected area networks is generally constrained by existing land-uses and location of current reserves, such that an optimal design is not possible. Given these practical limitations inherent to the conservation planning process, I applied a replacement cost analysis to quantify the change in the average level of representation given that the optimal solution is not possible (Cabeza & Moilanen, 2006). Specifically, I performed a biological cost inclusion analysis where current protected areas were forcibly included into the solution to evaluate the change (decrease) in level of representation compared to the optimal solution. Current protected areas included those classified as IUCN category I through VI (IUCN & UNEP, 2013) and only protected areas within the boundary of current and future dispersal modified SDM projections were retained. I expected that inclusion of existing protected areas would result in higher inclusion costs and lowered representation of forested habitats for breeding relative to nonbreeding priority solutions, in part a function of the larger non-forested areas captured by protected areas across the northern hemisphere. I compared inclusion costs by reporting the mean proportion (across all bird species) of the distribution of each species retained as a function of the percentage of land retained for protection (i.e. priorities).

5.3.4   Simulation experiments and analyses

To address the sensitivity of temporally dynamic spatial priorities under climate change to the inclusion of biotic features (i.e. habitat dependencies) I integrated biotic features applying two approaches. First, due to the prevalent use of climatic suitability as mapped distributions for priority assessments, I compared global priorities developed using predictive outcomes from abiotic versus biotic distribution models. Abiotic models consisted of climate variables (see SDM section) whereas biotic models included percent forest cover in addition to the climate predictor representative of the dominant habitat association among all modeled species. These separate classes of predictive models formed the inputs and unit of analysis within the Zonation framework.

I performed a total of 12 prioritization experiments that included: two seasonal ranges, two SDM predictions (abiotic and biotic), three time periods of analysis (2000,

2080, and 2000-2080), and with and without current protected areas. Results were summarized across all biodiversity features based on the average representation across the top 10% priority areas for breeding and nonbreeding ranges, independently. I performed multiple comparisons to quantify the influence of inclusion of the biotic feature via the SDM predictive outcomes and to illustrate differences in spatial dynamics over time due to potential climate changes between the seasonal ranges. To track changes in representation of direct habitat features across seasonal ranges, I quantified the percentage of forest cover captured by each solution of the 12 prioritizations. As a measure of spatial overlap between priority landscapes, I applied the Jaccard index (J), which is defined as the intersection between two grid layers divided by their union ($J = X \cap Y / X \cup Y$). The index varies between 0 and 1 with higher values indicative of higher spatial overlap.

The spatially disjunct distributions of long-distance migratory bird seasonal ranges present a natural experiment to examine the spatial dynamics of priorities under potential future climate changes across large latitudinal gradients. Topographical constraints, land-use legacies, and spatial distribution of current land-uses likely influence both the percentage of forest habitat contained within priority solutions, and potentially interact with the projected range shifts as a result of climate changes. I calculated the proportion of cells identified as priorities within 200 km wide latitudinal bands over three mutually exclusive periods (in the current period but not in the future, in the future to the exclusion of current priorities, and their intersection). Similarly, I calculated the proportion of cells identified as priorities against totals for each country to estimate the potential shifting of representation across political boundaries, underscoring the necessity of collaborative transboundary planning.

5.4 Results

5.4.1 Inclusion of biotic factors

The degree of spatial overlap as measured by the Jaccard index of similarity between abiotic and biotic classes of SDM priority landscapes illustrates two clear trends. The results in the following two sections reflect analyses performed without integrating the

current protected area reserve network. First, overall similarity between the two model classes was qualitatively modest to low (ranging from 0.58 to 0.29), depending on the period of analysis, regardless of the seasonal range under consideration (Table 5.6.1). This underscores the sensitivity of priority areas resulting from the inclusion of a biotic predictor variable within the SDM. Second, similarity between abiotic and biotic classes of priorities was lower in the future (2080) relative to the current (2000) landscapes for both seasonal ranges, illustrating divergence between spatial priorities due to the inclusion of a biotic predictor compounded by projected climate change (Table 5.6.1). Spatial congruence between abiotic and biotic priority landscapes for the 2000 and 2000-2080 time periods (where both periods and spatial connectivity between periods were considered simultaneously) were highly aggregated within core areas regardless of seasonal range, although this pattern was more pronounced for breeding season priorities. This pattern is in part reflected by the higher proportion of like adjacencies for breeding priorities and abiotic relative to biotic priorities regardless of seasonal range, where a higher value is indicative of more spatial aggregation (Table 5.4.1). By contrast, the low Jaccard index between abiotic and biotic 2080 priority landscapes was reflected in more fragmented areas of overlap, a pattern captured by the increasing number of spatially distinct areas (i.e. patches) and less core area with the 2080 priorities (Table 5.4.2). Divergence between abiotic and biotic priority landscapes for the 2080 period was spatially structured and especially pronounced in the south-eastern US and north-western portions of the breeding range, which coincide with range boundaries for a large number of species.

The degree to which the top 10% priority areas captured forest cover varied as a function of both SDM class used as input to the prioritization and with potential future climate changes (Fig. 5.7.1). Based on prioritizations that do not consider pre-existing protected areas, the mean percent forest cover summarised across each top 10% priority solution was consistently higher for all solutions based on the biotic SDMs, except for the 2000 breeding solution. Nonbreeding range priorities resulted in lower mean percent forest cover relative to the breeding range with coverage declining for both ranges over time with projected climate change. Furthermore, priority landscapes based on biotic

SDM outcomes for each seasonal range consistently selected fewer cells that contained no forest cover for each year of analysis. Despite the apparently small differences in number of cells with 0% forest cover, this translates into modest areal differences for both seasonal priorities due to the global scale of the study area. For example, the spatial priorities based on the biotic breeding models resulted in 0.38% (7,200 km^2) of the priority landscapes containing no forest, compared to 1.45% (27,400 km^2) of priority landscapes based on abiotic models.

5.4.2   Spatial dynamics of priority landscapes over time

Comparing the similarity of solutions between all pairwise combinations of the three periods of analysis, current (2000), future (2080), and both periods considered simultaneously (2000-2080), resulted in generally low Jaccard values (< 0.5) highlighting that spatial priorities identified in the current period will not be robust to future climate change across each seasonal range (Table 5.4.1). There was greater spatial divergence among breeding priorities based on temporal comparisons when compared with nonbreeding Jaccard values, reflective of the large projected latitudinal shifts in species distributions under future climate change for the breeding ranges (Table 5.4.1). By contrast, the low spatial overlap of nonbreeding priorities between current and future periods produced more heterogeneous patterns in spatial discrepancies along latitudinal, longitudinal, and elevational gradients. However, higher Jacccard values between 2000 and 2000-2080 priorities relative to 2000 and 2080 priorities suggest that by planning for both current with future climatic conditions by integrating uncertainty controlled climate projections can assist in identifying spatially concordant regions (consensus areas with climate change).

The representation of priority areas varied by latitude but the strength of this relationship was influenced by the seasonal range under consideration. Across the breeding ranges, there was a clear latitudinal gradient in the locations of priority areas whereby the proportion of 2000-only priority areas declined with increasing latitude. However, this pattern was reversed for future priorities (2080-only): the proportion of 2080-only priority areas varied positively with increasing latitude (Fig. 5.7.2 a – b). This

switch in temporal representation of priorities by latitude was less evident and spatially more complex when considering the nonbreeding season (Fig. 5.7.2 c – d). While the nonbreeding range priorities varied less clearly with latitude under future climate change, spatial conservation priorities have the potential to shift across national boundaries as species track suitable climates (Fig. 5.7.3). Across the nonbreeding ranges, conservation priorities for the current period were spread over a relatively small land area with large variation in proportional representation of the top 10% priority areas across 20 countries (Fig. 5.7.3). When considering future climate change, regions of high priority have the potential to shift across national boundaries as species track suitable climates. This pattern is clearest across the breeding ranges as there is a complete switch in national responsibility between Canada and the USA. Within nonbreeding ranges, a shift in priority areas with climate changes translates into transference of national responsibility for certain countries more than others.

5.4.3   Replacement cost analysis

Spatial congruence between abiotic and biotic SDM priority landscapes increased with the inclusion of protected areas. Nonbreeding range priority landscapes had a consistently higher Jaccard index relative to breeding priorities, illustrating the influence of the higher proportion of protected areas within the nonbreeding relative to breeding region. Temporal changes in priority landscapes due to climate-induced range shifts led to lower 2080 indices of spatial similarity relative to 2000 for both seasonal priorities. The inclusion of protected areas into the priority solution influenced mean percent forest cover of all solutions, however, directionality of change varied by seasonal range. For all breeding solutions spanning the three periods of analysis, mean percent forest cover decreased when protected areas were forcibly included, while the nonbreeding solutions exhibited the opposite trend (Fig. 5.7.1). Despite the increase in mean cover for the nonbreeding regions, the percentage of grid cells containing no forest cover increased in all periods except for the 2080. Overall, integrating protected areas into priority solutions under projected climate change resulted in marginal changes to the mean percent forest cover and the percentage of grid cells with 0% forest cover contained within each solution compared to the current (2000) period.

Regardless of seasonal range, there was a consistent biological cost (i.e. lower mean proportion of all species distributions retained, or, lower average level of representation) of including protected areas within the solution for the current period, which was highest at low levels of landscape retention (Fig. 5.7.4). Generally, for any given level of landscape removed, the average level of representation was higher for nonbreeding versus breeding priorities. Furthermore, the biological cost of including protected areas was consistently higher for nonbreeding relative to breeding priorities across all periods of analysis, in particular at the 90% level of landscape removal. This occurred despite a higher average mean percent forest cover retained within the nonbreeding solutions (both model classes) with the protected areas forcibly included. Interestingly, the average representation across all bird species was higher for the nonbreeding abiotic relative to the biotic model, however, the abiotic solution captured less average percent cover of forest. Average representation of biodiversity features for the breeding season was not sensitive to the selection of SDM classes; however, at the top 10% of priority areas breeding solutions generally had a low average level of representation. This was further reduced when protected areas were included.

5.5 Discussion

Vulnerability assessments and the identification of spatial conservation priorities for migratory species requires inclusion of all seasonal habitats to ensure protection is conferred across all biologically relevant portions of the annual cycle. Despite this, few valuations adopt such a comprehensive assessment, which brings into question the capacity of these prioritizations to achieve conservation goals (Small-Lorenz *et al.*, 2013a). Many migratory species reside seasonally in regions characterized by large variation in land-use and land-cover patterns, biogeography, density of national political boundaries, and socio-economic-cultural facets that further challenge the planning and implementation of conservation priority areas. These disparate regions are further characterized by spatially distinct future climatic changes both in terms of departures from current climates and the advent of novel climates (Williams *et al.*, 2007, Mora *et al.*, 2013), which can influence different portions of the annual cycle. I showed that for Nearctic-Neotropical migratory birds future climate changes influenced the pattern of

spatial priorities in asymmetric ways depending on the seasonal range under consideration; high latitude breeding priorities resulting in large northward shifts, while differences in nonbreeding priorities were characterized by more complex heterogeneous patterns. Regardless of the seasonal range under consideration, representation of priority areas shifted spatially as a result of future climate change leading to variation in responsibility across international boundaries. By accounting for SDM algorithm uncertainty, the type of GCM through a combination of consensus and distribution discounting methods, these results underscore the sensitivity of spatial conservation priorities to the inclusion of a habitat-based biotic predictor within the SDMs. Below I discuss the implications of this cascading influence of a single biologically relevant predictor variable for conservation planning based on SDMs and how this might impact decisions related to conservation actions and inform transboundary management issues.

5.5.1   Influence of biotic factors

Including biotic predictors in SDMs developed for animal species reliant on vegetation resulted in substantive spatial differences in conservation priorities relative to inputs based on abiotic-based SDM predictions, with differences amplified when climate changes were considered. By accounting for uncertainties in SDM algorithms and choice of GCMs, I were able to isolate the influence of the inclusion of a habitat factor of importance for the focal species under consideration on spatial conservation priorities. Incorporating resource-based predictors (i.e. biotic vegetation factors here) into SDMs minimizes the potential for over-estimating species distributions and potential range shifts under future climate changes (Heikkinen *et al.*, 2007, Schweiger *et al.*, 2008, Kissling *et al.*, 2010). When such limiting variables are not included as predictors, this introduces false presences (i.e. higher commission error rate). Focusing on breeding range SDMs, which used presence-absence occurrence data (nonbreeding used presence-background); the average omission error rate was relatively similar between abiotic and biotic SDMs, while the commission error rate was higher for abiotic SDMs relative to biotic SDMs (Naujokaitis-Lewis et al Chapter 2). This suggests that the addition of the vegetation feature included important information influencing species occurrences, specifically the false positive rate, which minimized overprediction in geographic space

relative to the abiotic models (Fielding & Bell, 1997) (the rate at which the model incorrectly predicts presences). This resulted in quantifiable differences in the spatial pattern of priority areas both under current climates and when considering future projections. In the context of conservation planning, commission errors may be more costly than omission errors (Lobo *et al.*, 2008), whereby model outputs with higher commission errors will result in selection of areas not suitable or relevant for conservation, which could result in high costs from both biological and economic perspectives (Rondinini *et al.*, 2006). In combination with the posterior analyses indicating that biotic priorities captured higher average percent cover of forested habitats, these results highlight the importance of including biotic predictors in SDMs for vegetation dependent species.

Spatial incongruence between abiotic and biotic SDM derived priorities were amplified when projected climate change was considered. I showed that when accounting for variability associated with both SDM algorithm and GCM used, the addition of a single biotic predictor can have cascading influences on the selection of spatial priority areas for conservation under climate change. Identification of climatically suitable priority areas achieved lower representation of forested habitats required for vegetation dependent species. All biotic-based priorities retained more average percent forest cover and selected fewer grid cells devoid of forests, reinforcing the importance of inclusion of resource limiting factors even for SDMs developed at broad scales. This was particularly evident for nonbreeding range priorities across all periods of analysis, possibly explained by forested habitats being more limited in these regions. Importantly, biotic-based priorities that considered climate changes always captured higher average percent cover of forested habitats, suggesting that abiotic-based priorities may lead to inefficiencies due to selection of regions devoid of habitat. Large anomalies in future species distributions under climate change projections is a recognized issue resulting from different parameterizations of GCMs, type of SDM algorithm, and the choice of variables used in the SDMs (Beaumont *et al.*, 2005, Beaumont *et al.*, 2008, Diniz-Filho *et al.*, 2009, Garcia *et al.*, 2011). These results further support the role of variable selection on SDM predictive outcomes and demonstrate how the addition of an ecologically relevant

predictor variable into SDMs translates into differences in spatial conservation priorities that are magnified under projected climate changes. Overall, this suggests that conservation priorities identified using only predictive models estimating the climate envelope of vegetation-dependent species will result in the inefficient allocation of conservation resources via the selection of regions with inadequate amounts of habitat.

This study focused on quantifying the seasonal differences in spatial conservation priorities under climate change for a set of long-distance migratory birds and illustrated the sensitivity of priorities to the inclusion of habitat-based biotic factors. From a methodological perspective, integrating biotic predictors directly into the SDMs may be advantageous when data permits in terms of spatial coverage and resolution. When this is the case, these models establish links between species occurrence and environmental and habitat features and thus contribute to reducing both commission and omission errors (Chapter 2). This allows direct modeling and projection of potential consequences of dynamic changes in land-use and climate into spatially explicit predictive outcomes (e.g., Barbet-Massin *et al.*, 2012b, Schweiger *et al.*, 2012, Martin *et al.*, 2013), which can subsequently be used as inputs into spatial conservation priority assessments. Further, in cases where detailed knowledge of specific habitat preferences is unknown, it may be advantageous to include hypothesized representative predictors within SDMs to model the expected relationship. A complementary method is to include vegetation or other habitat elements in the conservation priority process via a habitat filtering approach as *a posteriori* analyses after SDM development (e.g., Faleiro *et al.*, 2013, Lemes & Loyola, 2013). This may be beneficial in addition to or in place of inclusion as predictor variables under the following situations: (1) where data are not of consistent spatial or temporal coverage (Faleiro *et al.*, 2013), (2) where over-prediction and false positives are of concern in SDM predictive outcomes (e.g., when climate variables have a disproportionate influence on predictive outcomes resulting in high errors of commission even when habitat variables are included, or due to use of coarse-grained data; (Rondinini *et al.*, 2006, Hermoso & Kennard, 2012)), and (3) when more refined priorities are required in particular for smaller scale assessments reflecting scale of many decisions (Wiens & Bachelet, 2010) or where species are patchily distributed (Schwartz *et al.*,

2006). Evaluating the relevance of each method requires at a minimum careful interrogation of the SDM outcomes with a particular emphasis on commission and omission error rates, where applicable. Regardless of the method, I found cross-examination of priority assessments using a variety of landscape-level metrics, spatial indices of similarity, and spatially explicit map-based comparisons enabled a deeper understanding of the limitations associated with abiotic-derived SDMs.

5.5.2 Shifting spatial priorities across political boundaries under climate change

Migratory species present a unique challenge for conservation planning as the often wide distances between seasonal ranges result in threat dynamics structured across their seasonal ranges. These results point to clear latitudinal shifts in priority areas under future climate changes across the breeding range while nonbreeding range priorities exhibited large spatial shifts with more complex patterning. These asymmetrical patterns of shift under climate change resulted from the potential range shifts in response to changing climates, which follow expected patterns across latitudinal gradients. Across breeding priorities, there is complete reversal in the level of responsibility of each country into the future. With a high density of national borders across the nonbreeding ranges, the variability in priorities under climate change led to shifting responsibilities both within and across political boundaries. This shifting representation of species' distributions across multiple national boundaries presents additional challenges for coordination and implementation of conservation plans. Currently, conservation and management of migratory species requires international collaboration as population-level threats and processes are linked across seasonal ranges (Holmes, 2007). The anticipated spatial shifts in priority areas across political boundaries under climate change further emphasize the need for collaborative actions to conserve wide-ranging migratory species. Consideration of socioeconomic and political factors that influence collaborative conservation will be required to assess both willingness and ability of country involvement (McDonald & Boucher, 2011). Such factors, such as likelihood of establishing collaborations among various stakeholders can be incorporated into both scoping and quantitative analysis phases of the systematic conservation planning process (Pressey & Bottrill, 2009, Micheli

et al., 2013). An additional factor likely to provide increased incentive for international collaboration is through the identification of spatially concordant priority areas that integrate priority species endemic to Central and northern South America alongside nonbreeding ranges of Nearctic-Neotropical migrants (Berlanga *et al.*, 2010).

5.5.3   Current and future effectiveness of protected areas

The distribution of protected areas is not spatially homogenous across the seasonal ranges nor do they currently capture similar proportions of forest cover, resulting in asymmetrical benefits from protected areas both currently and under future climate changes. Over the breeding season, the inclusion of protected areas resulted in much lower mean coverage of forests across priority areas despite the prevalence of climatically suitable areas. This emphasizes the tendency for protected areas across the breeding range to cover non-forested areas, not unexpected given their spatial bias at high latitudes towards steep, rocky, and icy regions (Joppa & Pfaff, 2009). Despite the non-optimal placement of current protected areas denoted by the large decrease in biological value when priorities are constrained to include the protected areas, inclusion of current protected areas in the nonbreeding range resulted in increased retention of forest cover. This might have occurred as a result of including protected areas that overlapped with current and future projections of species distributions, some of which occurred on the margins of current species distributions where climate-habitat suitability was lower (e.g. portions of Venezuela). This suggests that focusing on vegetation only to guide reserve selection could be misleading but requires further exploration. Regardless, inclusion of protected areas across the nonbreeding range resulted in much larger differences in average biological value (i.e. average level of representation) when 10% of priority landscapes were retained. There were many more biologically valuable sites but selection was prevented by the inclusion of protected areas, especially across nonbreeding ranges, where average representation was higher at the 10% level, possibly related to generally smaller size of nonbreeding relative to breeding range.

5.5.4   Limitations and future opportunities

There are a number of limitations with this approach, which serve to highlight opportunities for future work. While I considered the future spatial dynamics of global climate change, I assumed that percent forest cover remained static over time. Rates and magnitude of change in vegetation amount and configuration could occur via a direct pathway whereby climate change influences vegetation growth or, loss of forested habitats might occur independent or in interaction with climate changes (Mantyka-Pringle *et al.*, 2012). Loss of forested habitats through conversion to alternative landcover types is a formidable threat expected to persist into the future (Sala *et al.*, 2000), with spatial patterns of threats likely to differ regionally with the potential for interactions between multiple stressors (Brook *et al.*, 2008, Mantyka-Pringle *et al.*, 2012). Global spatial variation in recent and future land-use conversion could lead to loss of habitats disproportionately affecting regions across a given seasonal range (Jetz *et al.*, 2007, Hansen *et al.*, 2013). For example, (Jetz *et al.*, 2007) modeled the projected effects of the interaction between climate and land-use change on global bird distributions and found that climate change had a disproportionate influence on future range contractions in temperate regions whereas land-use change was the primary driver of change in tropical regions. This emphasizes the need for seasonal range assessments for migratory species due to regional differentiation in threat dynamics. As changes in forest cover are likely to change dramatically over the period of analysis further work extending this line of enquiry would benefit from a comparative analysis including this dynamic threat. In addition, the integration of migratory connectivity, the spatial linkages between populations across different stages of the life-cycle, will be a critical step to identifying priority areas that are able to conserve populations representative of these connections (Martin *et al.*, 2007), however, limited empirical data and likely species-specific patterns currently hinder its inclusion.

5.5.5   Conclusions

Given the lack of uniformity in direction and magnitude of threat dynamics, assessing spatial patterns of vulnerability across all habitats required over the annual cycle of

migrant species is crucial for initial risk evaluations and for conservation priority setting. Priority setting for conservation currently and under the threat of climate change requires consideration of seasonal habitats that support migratory species across their annual cycle. For long-distance migratory birds, both the distribution of habitat features and the potential threat dynamics of changing climates vary in heterogeneous patterns across their seasonal ranges. Identification of climatically suitable priority areas does not necessarily select regions with habitat required for vegetation dependent species. Thus excluding biotic factors from SDMs is likely to misinform conservation priorities based on predictive outcomes through identification of priorities that actually constitute false positives. This study advances our understanding of the sensitivity of conservation priorities to the inclusion of biotic factors into the underlying SDMs that inform the spatial quantitative portion of the planning process. Understanding the spatial dynamics of priorities with climate change across seasonal ranges is imperative for operationalizing conservation actions because of concordant changes to the level of responsibility of nations. Developing stronger predictive science that overcomes current methodological limitations and pursuing research to better inform management decisions arising from the application of SDMs (Schwartz, 2012, Guisan *et al.*, 2013) will help advance goals of biodiversity conservation. Migratory species represent opportunities to develop our collective capacity for collaboration requiring the global community to move towards accepting responsibilities for shared resources in a dynamic world.

5.6   Tables

Table 5.6.1 Jaccard index of similarity between maps based on top 10% priority areas for abiotic and biotic SDMs, and multiple time comparisons (2000 to 2080, 2000 to 2000-2080 where both periods are considered simultaneously, and 2080 to 2000-2080). Pairwise comparisons are delineated by seasonal range both with and without protected areas (IUCN category I-VI).

Type of comparison		Breeding		Nonbreeding	
		without PAs	with PAs	without PAs	with PAs
Abiotic with biotic	2000	0.55	0.78	0.58	0.93
	2080	0.29	0.63	0.30	0.80
	2000-2080	0.44	0.69	0.45	0.83
2000 with 2080	Abiotic	0.17	0.55	0.23	0.89
	Biotic	0.12	0.51	0.23	0.80
2000 with 2000-2080	Abiotic	0.31	0.57	0.52	0.91
	Biotic	0.27	0.59	0.50	0.83
2080 with 2000-2080	Abiotic	0.33	0.59	0.36	0.91
	Biotic	0.33	0.58	0.37	0.97

Table 5.6.2 Comparison of landscape level statistics for abiotic- and biotic-based spatial conservation priorities for breeding and nonbreeding ranges across multiple periods of analysis, 2000, 2080, and 2000-2080 where both periods where considered simultaneously.

	Period of analysis	Nonbreeding		Breeding	
		Abiotic	Biotic	Abiotic	Biotic
Number of patches	2000	118	257	55	212
	2080	390	602	173	266
	2000-2080	249	355	152	308
Landscape shape index	2000	14.88	20.48	9.36	17.33
	2080	23.22	30.30	17.69	19.74
	2000-2080	19.40	22.96	14.66	19.72
Mean patch core area	2000	39.42	14.32	263.22	55.84
	2080	8.44	4.07	63.03	39.48
	2000-2080	15.49	9.58	80.88	34.75
Proportion like adjacencies	2000	0.73	0.65	0.87	0.78
	2080	0.61	0.52	0.77	0.75
	2000-2080	0.66	0.61	0.81	0.75

5.7   Figures
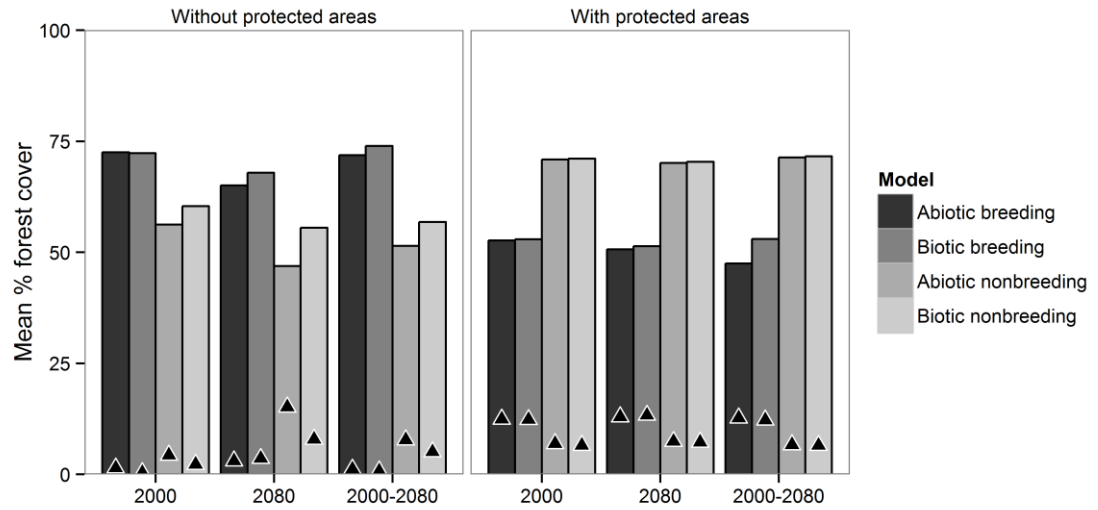
Figure 5.7.1 Mean % forest cover within the top 10% priority landscapes based on abiotic and biotic SDM outcomes for breeding and nonbreeding ranges, with and without protected areas. ▲indicates the % of cells within each experiment that contain no forests.
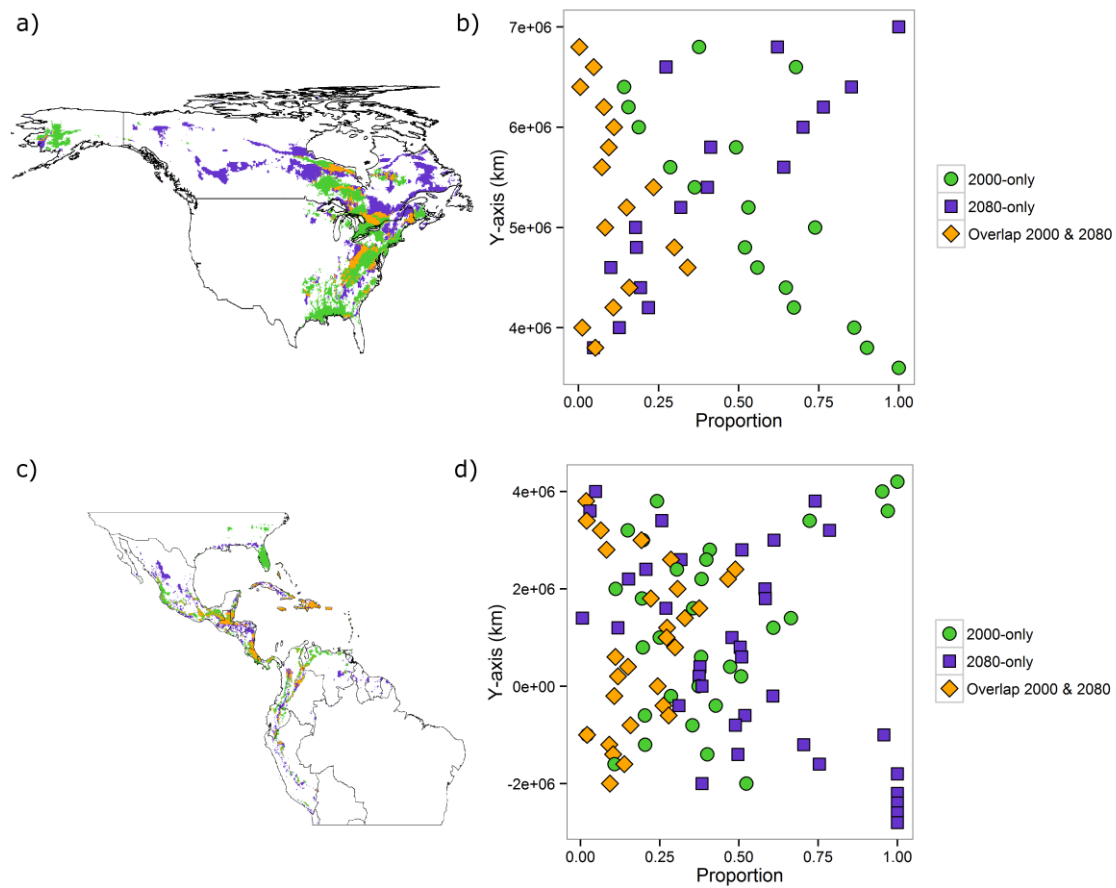
Figure 5.7.2 Top 10% priority areas for biotic class of SDMs for a) breeding ranges and c) nonbreeding ranges. Proportion of non-overlapping priority areas for the current (2000-only) and future (2080-only) periods and their intersection (overlap 2000 & 2080) relative to the total area identified as a priority for each 200 km latitudinal band for the b) breeding range and d) nonbreeding range, based on biotic SDM predictions.
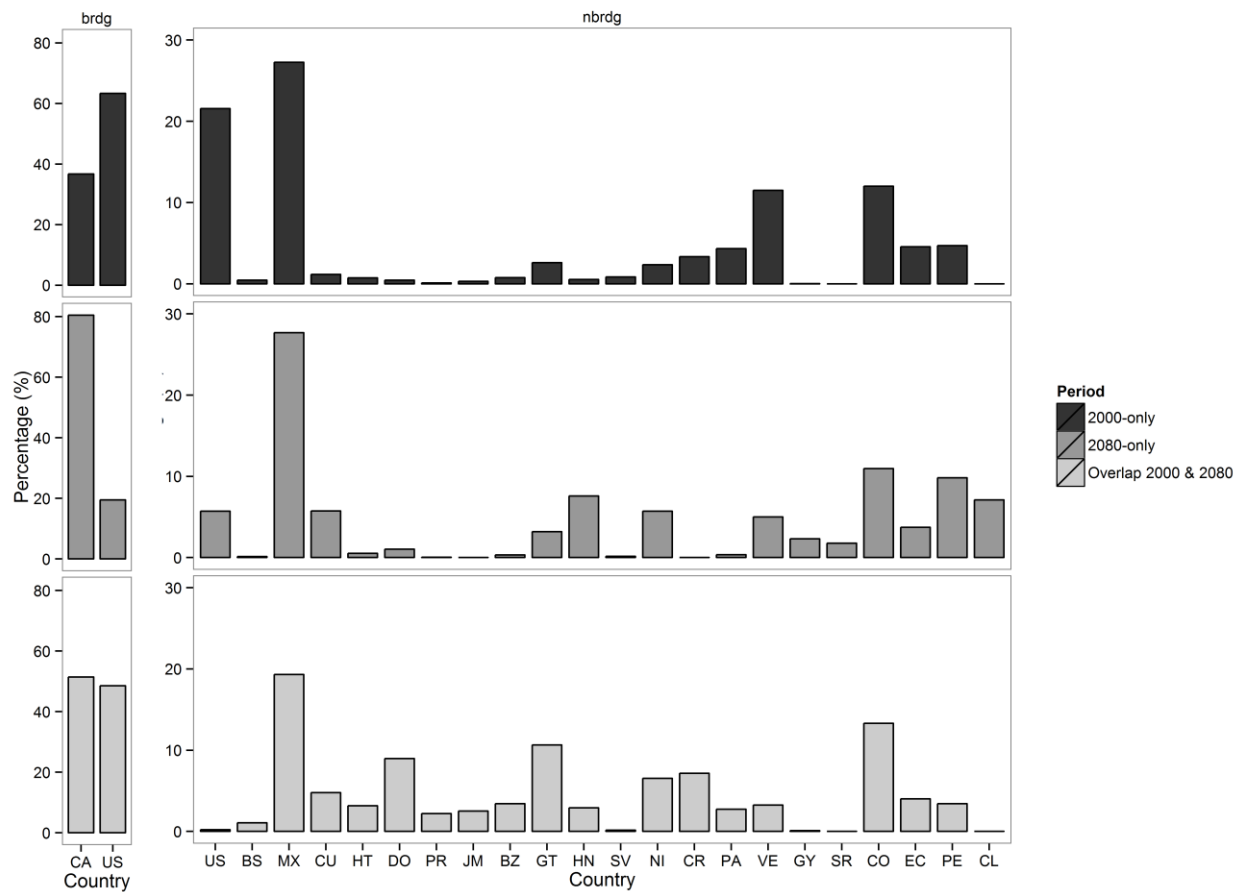
Figure 5.7.3 Proportional representation of priority areas for conservation across the nonbreeding range by country stratified by priority areas for (a) 2000-only, (b) 2080-only, and (c) those that spatially overlap with both 2000 and 2080. Countries are listed by breeding range (bars marked 'B') then nonbreeding (remaining bars), and then in decreasing order by average latitude of each country, calculated based on the country centroid in km using a Behrman equal area projection. Country abbreviations reflect ISO country standards.
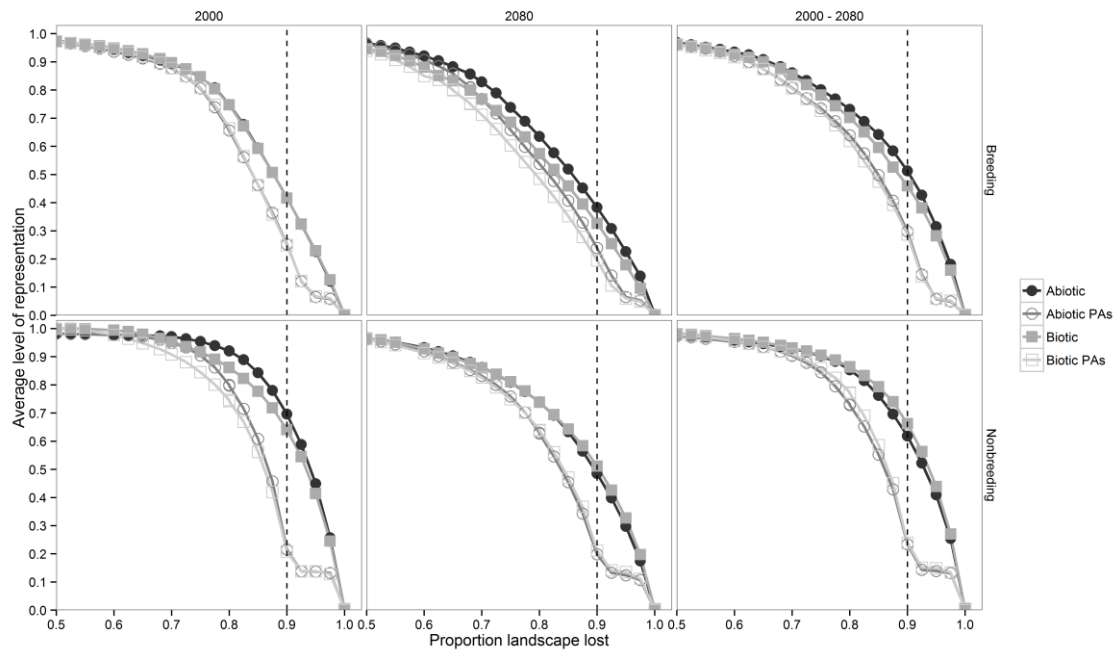
Figure 5.7.4 Average level of representation across all biodiversity features as a function of the proportion of landscape lost based on abiotic and biotic SDMs, both with and without protected areas (PAs) for breeding and nonbreeding ranges.

5.8   Appendix

Ensemble-based methods applied to derive consensus predictions among the five model algorithms used to predict species distributions under climate change for the 2000, 2050, and 2080 time period for the 28 species of Parulidae.

Consensus among the 5 modeling algorithms for each variable set for both the current and future predictions were based on a weighted mean of probabilities, where each algorithm was weighted proportional to its TSS score. The consensus among the GCMs was calculated based on the mean across projected probabilities of occurrence or relative suitability values, in the case of the nonbreeding models. Projections over the breeding season were converted to binary presence/absence data using a threshold maximizing the True Skill Statistic (Allouche *et al.*, 2006), which corresponds to the sum of sensitivity (proportion of presences correctly predicted) and specificity (proportion of absences correctly predicted) minus one. I applied a threshold of occurrence based on the 10% quantile of habitat suitability extracted from present-day occurrence records for the nonbreeding range outcomes, resulting in a less conservative threshold relative to the breeding season threshold of occurrence due to the lack of systematic sampling frame used to acquire the presence-only nonbreeding occurrence data.

5.8.1 Figures
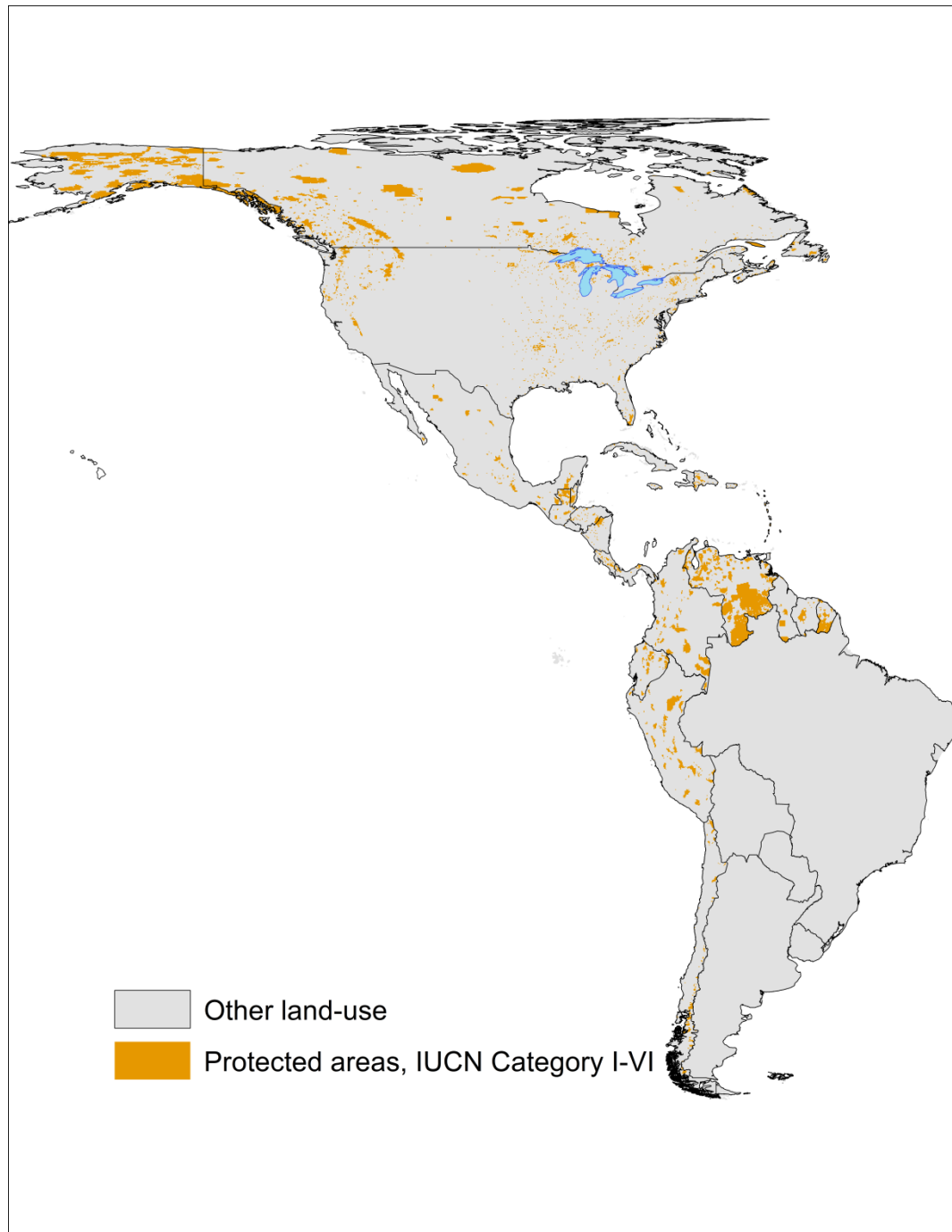
Figure 5.8.1 Map of protected areas, IUCN Category I-VI across breeding and nonbreeding ranges used in Zonation replacement cost analysis.

a)

b)

Change species richness

-20   -10   -5   0   5   10   20

c)

d)
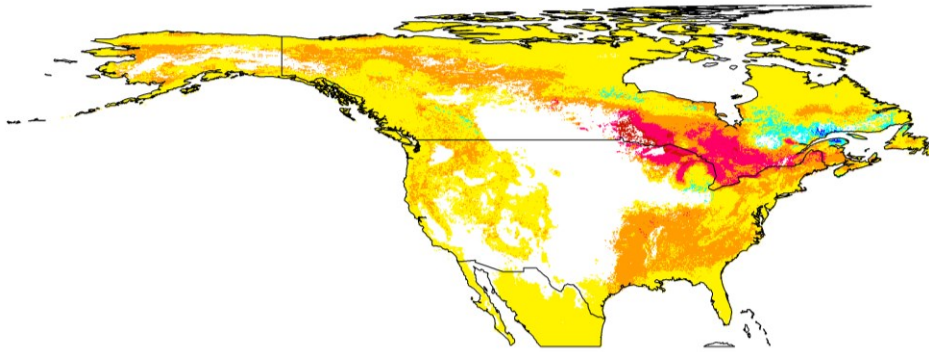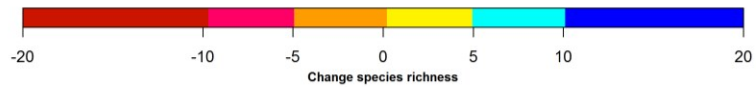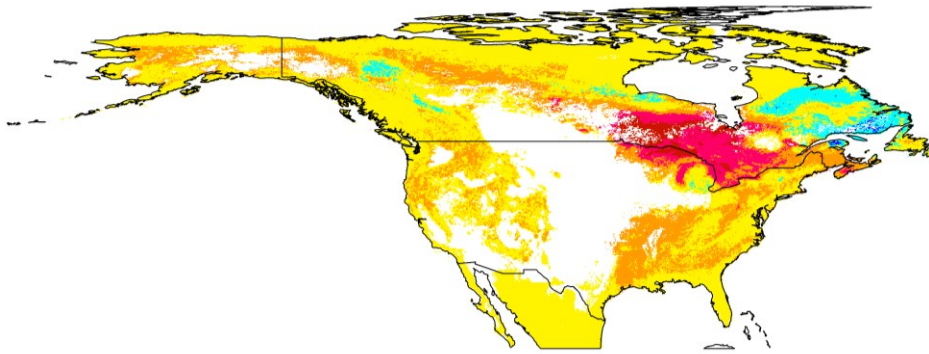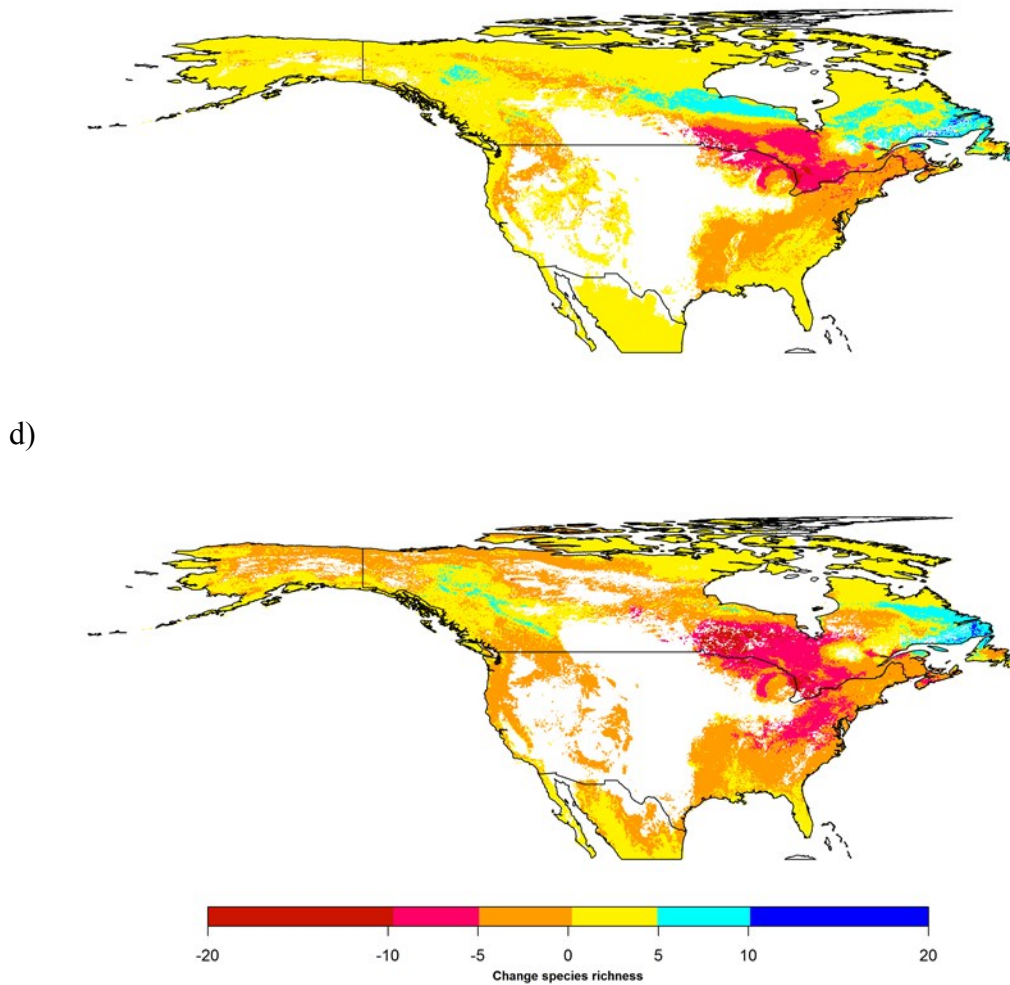
Figure 5.8.2. Projected changes in species richness across breeding ranges from 2000 (current) to 2080 projections for four different GCMs, a) CCMA, b) CSIRO-MK3, c) Hadley, and d) NIES-99. Species richness changes are based on SDMs using the climate-habitat variable set. Results for each GCM are summarized using ensemble across five model algorithms where each model is weighted proportional to the True Skill Statistic (TSS).

a)
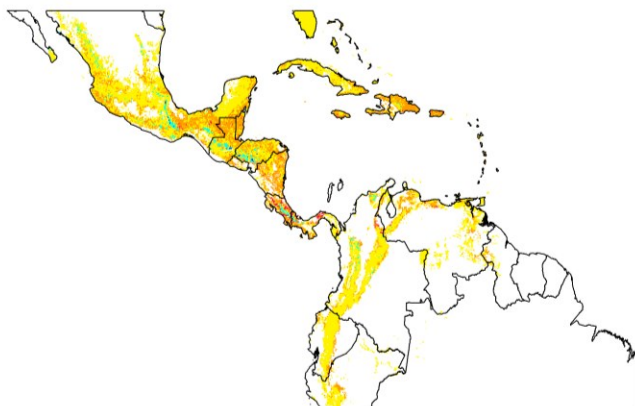
b)
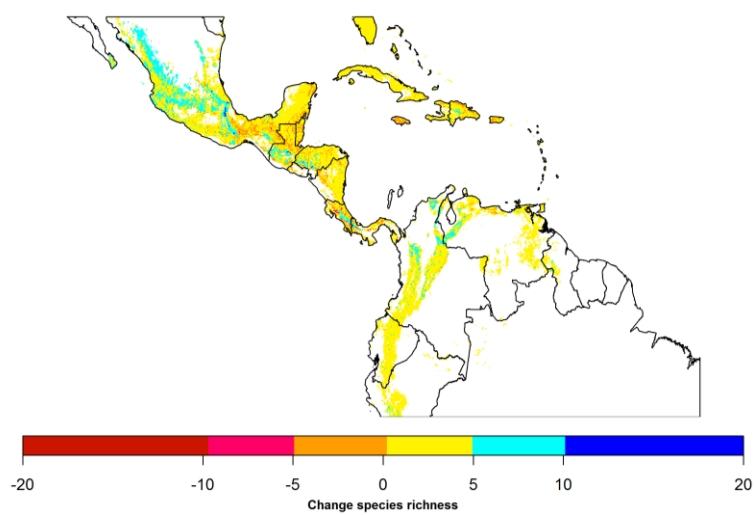
c)
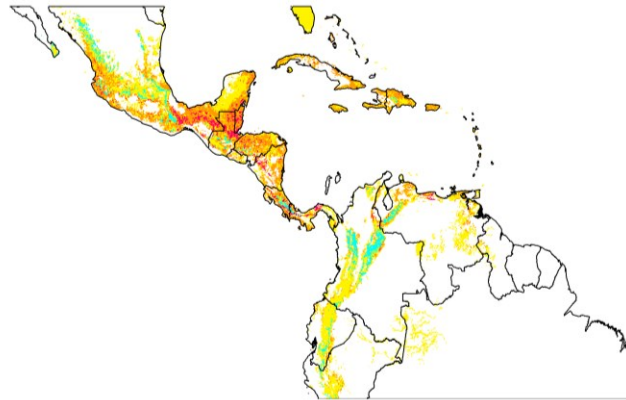
d)
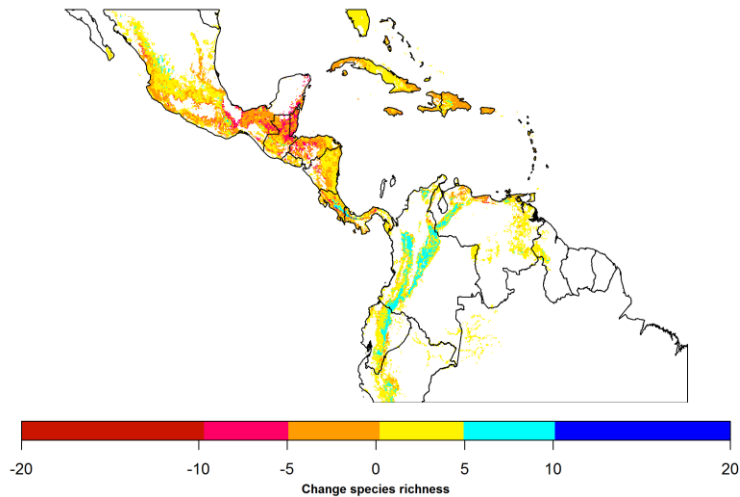
Figure 5.8.3. Projected changes in species richness across nonbreeding ranges from 2000 (current) to 2080 projections for four different GCMs, a) CCMA, b) CSIRO-MK3, c) Hadley, and d) NIES-99. Species richness changes are based on SDMs using the climate-habitat variable set. Results for each GCM are summarized using ensemble across five model algorithms.
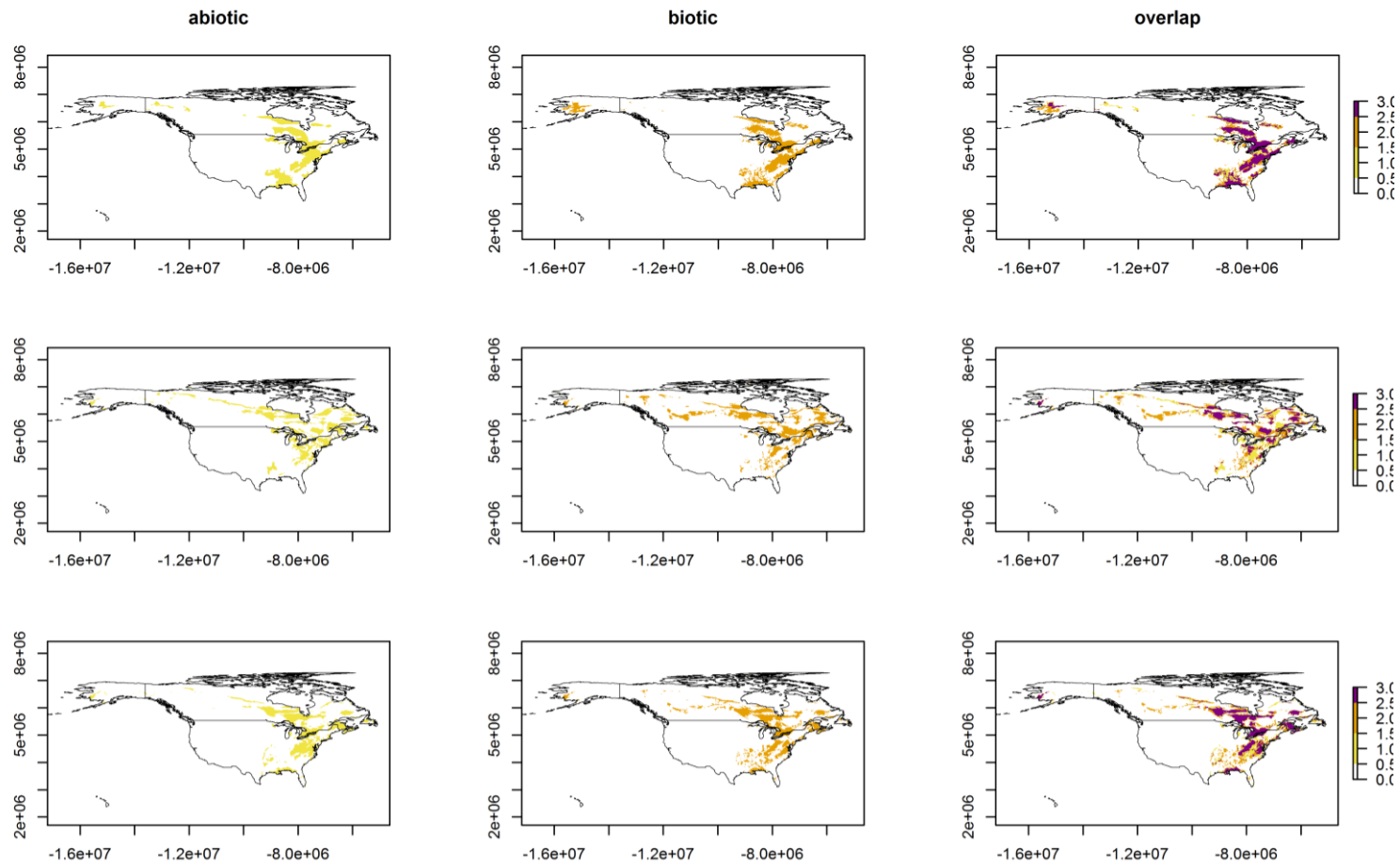
Figure 5.8.4 Comparison of breeding top 10% priority areas between abiotic and biotic SDMs. 1st row: 2000 priorities, 2nd row: 2080s priorities, 3rd row: both 2000-2080 priorities.
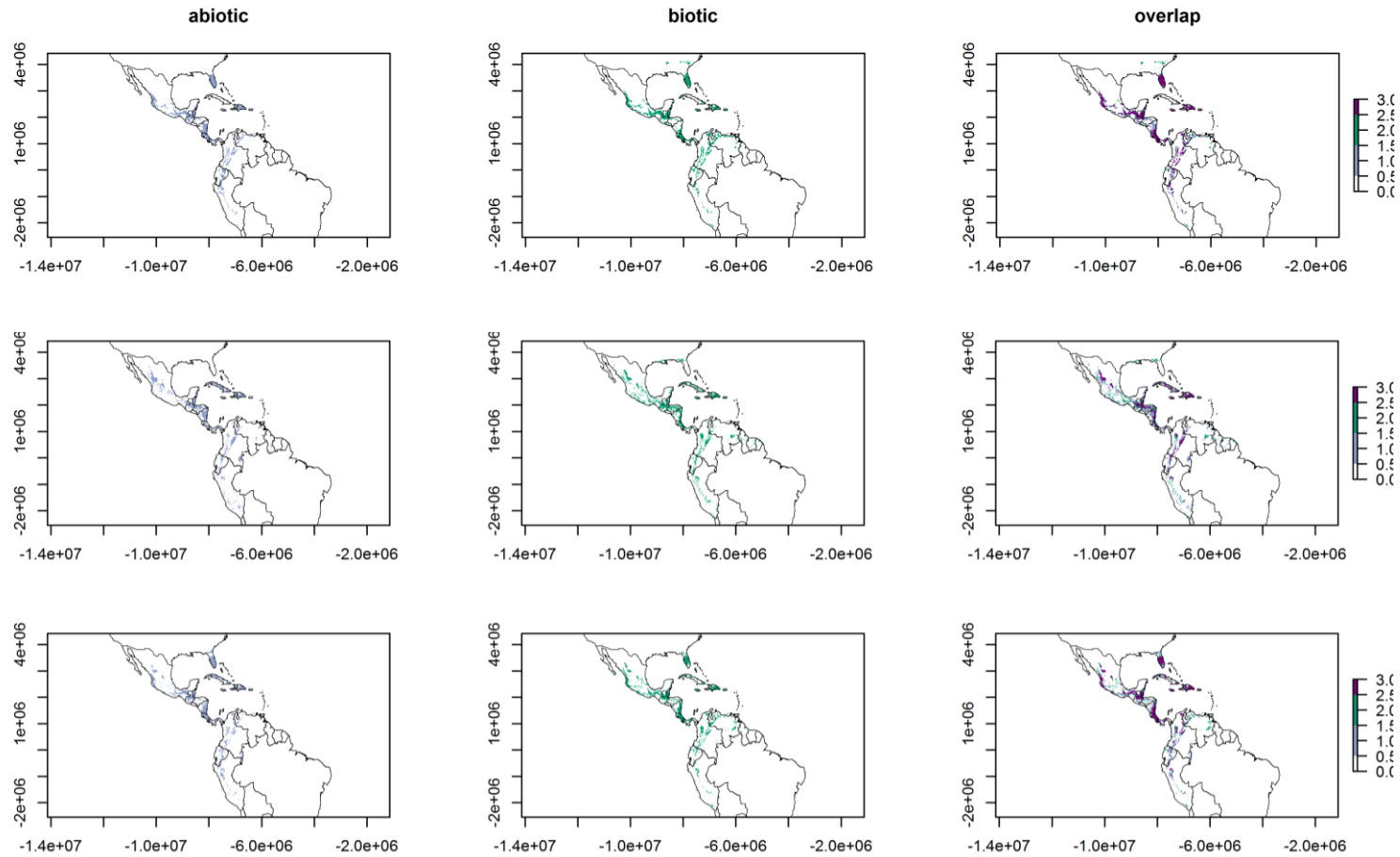
Figure 5.8.5 Comparison of nonbreeding top 10% priority areas between abiotic and biotic SDMs. 1st row: 2000 priorities, 2nd row: 2080s priorities, 3rd row: both 2000-2080 priorities.
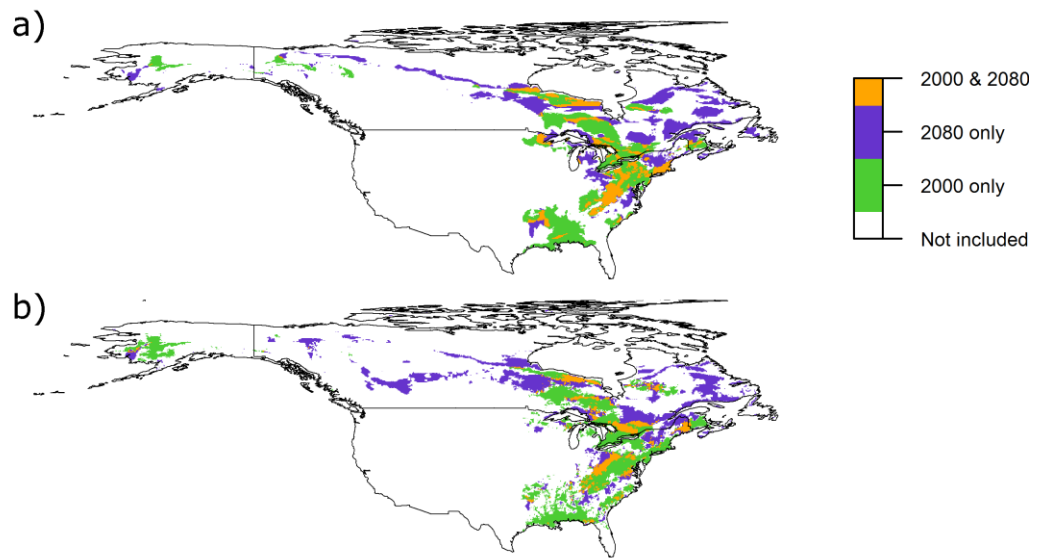
Figure 5.8.6 Top 10% priority areas based on a) abiotic SDMs and b) biotic SDMs across the breeding range. 2000-only and 2080-only: priority areas unique to the respective periods of analysis. 2000 & 2080 refers to priority areas that overlap between the two time periods.
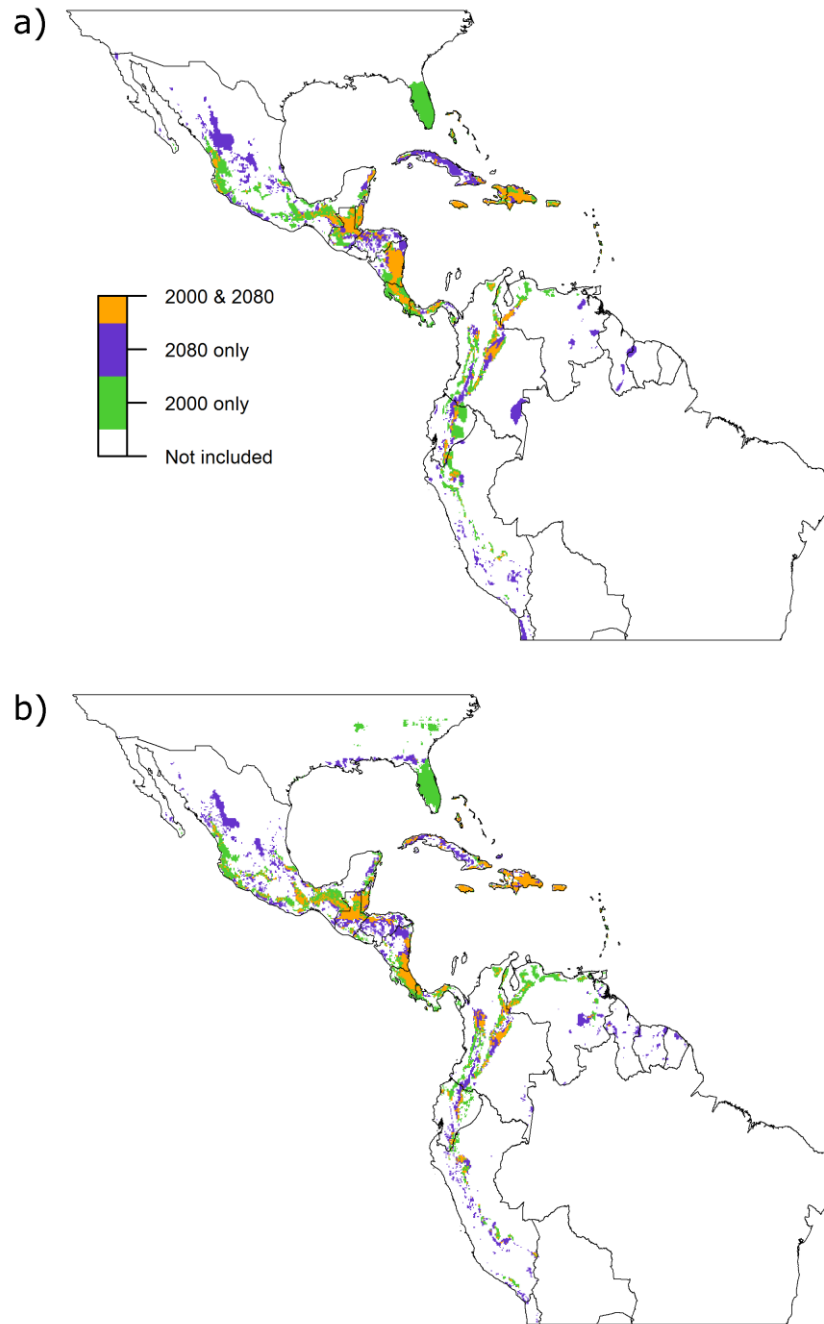
Figure 5.8.7 Top 10% priority areas based on a) abiotic SDMs and b) biotic SDMs across the breeding range. 2000-only and 2080-only: priority areas unique to the respective periods of analysis. 2000 & 2080 refers to priority areas that overlap between the two time periods.
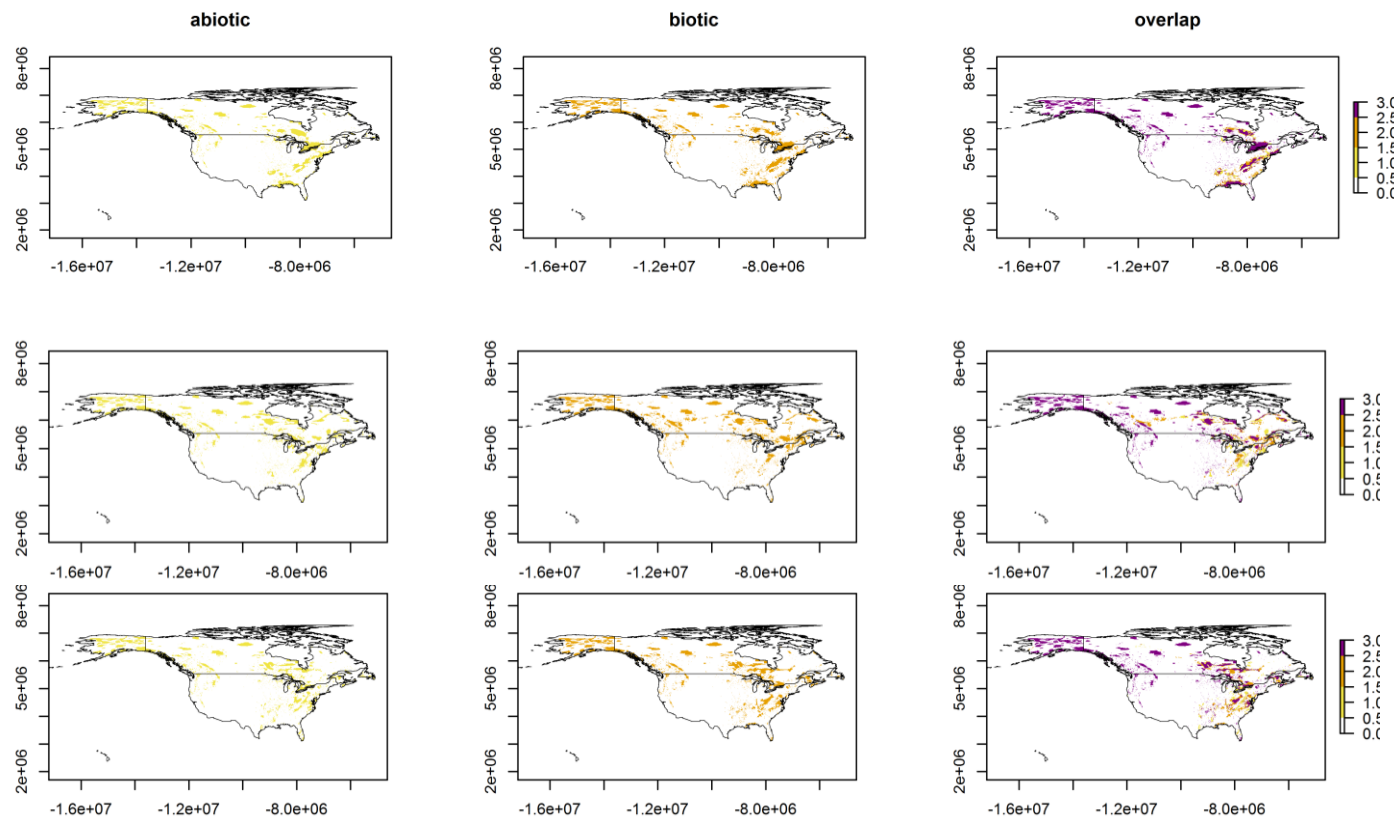
Figure 5.8.8 Comparison of breeding top 10% priority areas with current protected areas between abiotic and biotic SDMs. 1st row: 2000 priorities, 2nd row: 2080s priorities, 3rd row: both 2000-2080 priorities.
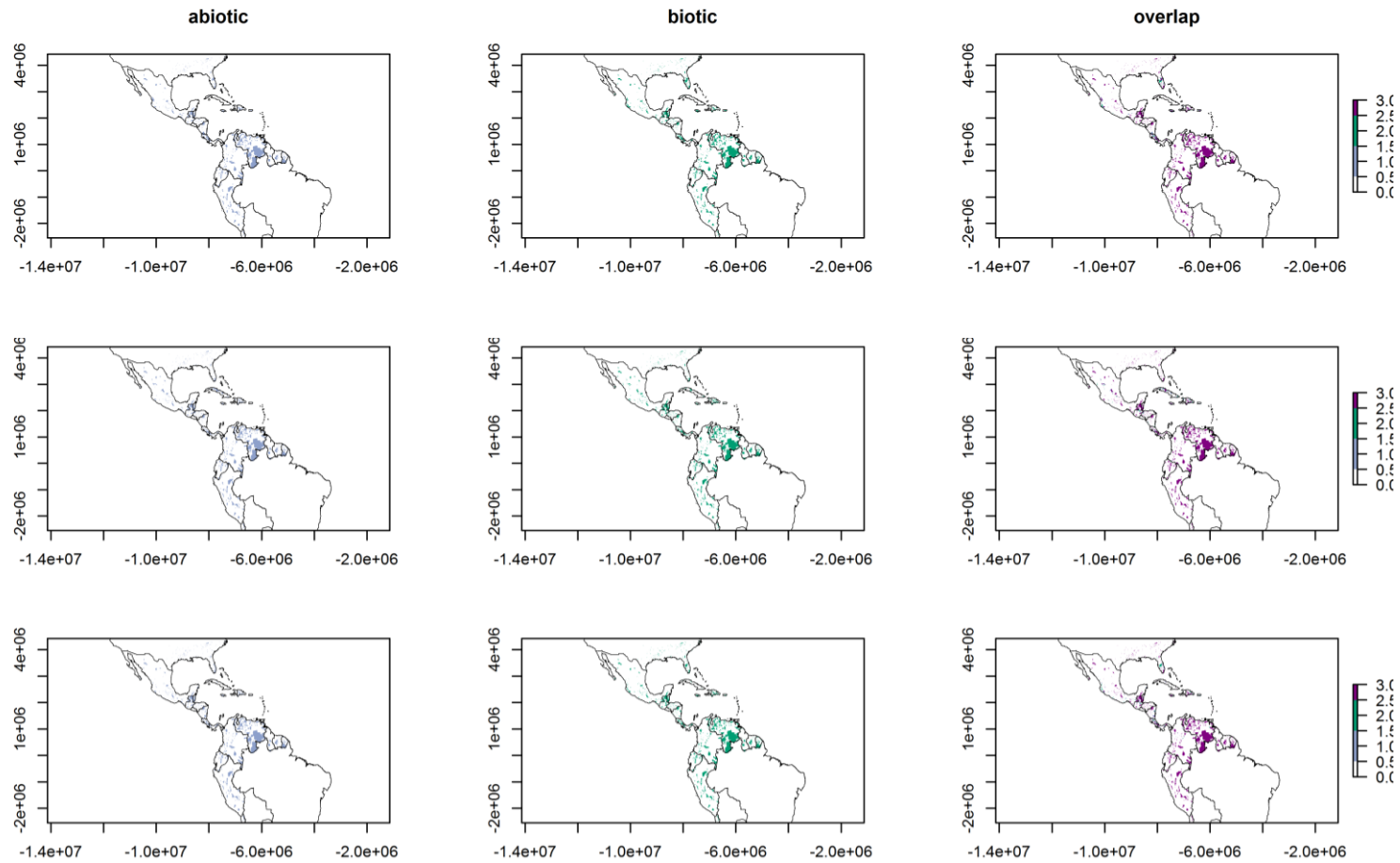
Figure 5.8.9 Comparison of nonbreeding top 10% priority areas with current protected areas between abiotic and biotic SDMs. 1st row: 2000 priorities, 2nd row: 2080s priorities, 3rd row: both 2000-2080 priorities.

6   **Discussion and Conclusions**

6.1 Synthesis

In this thesis, I have aimed to address the over-arching question: Why are species where they are, and how do we expect them to respond to dynamic threats? Despite the apparent simplicity of this question, it remains an outstanding problem guiding much ecological research given the direct implications under rapid global changes. I aimed to advance our understanding of the relative importance of climatic and non-climatic drivers on avian seasonal range dynamics, both in the past and in the future. I applied a diversity of modelling approaches that vary with respect to the degree of biological information, temporal scale of climate change and land-use dynamics, and spatial scale of analysis. A central theme of my PhD is the role and importance of uncertainty; I explicitly evaluated the influence of various types of uncertainty (Chapters 2, 4, 5), or accounted for uncertainty directly in the methods (Chapter 3). Multiple and common sources of uncertainty can influence predictive outcomes (Chapters 2, 3), robustness of inferences (Chapters 2, 3, 4), and has implications for management decisions focused on biodiversity conservation (Chapters 4, 5). Each chapter builds on the preceding by using methods that increasingly account for ecological processes that determine species' range dynamics.

In Chapter 2, I developed species distribution models to test the importance of including biotic vegetation factors in addition to abiotic (climatic) factors on predictive accuracy of species' current breeding and nonbreeding distributions, independently, for 33 species of long-distance migratory birds. I assessed the potential change in distributions under anticipated climate change and examined the relative contribution of different sources of uncertainty on range change metrics, including both latitudinal boundaries and proportional expected change in range size. Overall, the inclusion of biotic vegetation factors improved predictive accuracy on average across all species and both seasonal distributions. These results emphasize the importance of including covariates that capture biotic vegetation dimensions that relate to species' resource requirements, where vegetation functions as nesting habitat and proxy for food availability, even at broad spatial scales. My results suggest that projected climate change has the potential to influence directionality of range shifts dependent on the seasonal range and species' identity. Variation in both range change metrics were influenced by the type of model algorithm followed by choice of General Circulation Model. Key findings include (1) evidence for signals

of biotic vegetation factors at broad scales for this set of *Parulidae*, and (2) species-specific multi-directional projected range shifts regardless of season, and (3) strong seasonal differences in projected range shifts that may result in increased migration distance between seasonal ranges.

In Chapter 3, I tested the relative importance of multiple dynamic threats on annual variation in occupancy dynamics of two congeneric species. These dynamic threats are thought to represent the main drivers species range dynamics, namely habitat loss, climate change, and biotic interactions. I developed multi-year occupancy models over a 30-year period that account for detection errors in the sampling process and extended the model to integrate time-varying covariates. Inter-annual variation in estimated probability of extinction of both focal species was more strongly associated with fine-temporal scale habitat changes relative to climate. However, the probability of extinction in Golden-winged Warblers was most strongly related to presence of its congeneric species, the Blue-winged Warbler. While presence of a congeneric species was applied as a proxy for competition (Gotelli *et al.*, 2010), further work is needed to elucidate evidence for this mechanism. The methods applied in this chapter present an improvement on static species' distribution models (Franklin, 2010) by providing insights in the relationship between covariates and extinction and colonization dynamics that underlie range dynamics, while accounting for detection errors (Royle & Kery, 2007). Key findings of this work include: (1) the need to consider temporal scale of extrinsic environmental conditions as this may result in different inferences regarding the relative influence of multiple threats on broad-scale distributions, and (2) biotic factors influence species' colonization and extinction and are thus important for broad-scale range dynamics.

The use of species distribution models regardless of fine-spatial resolution can result in over-prediction of range shifts due to lack of uniform relationships with abiotic and biotic factors across broad scales. Using the Hooded Warbler as a case-study species in Chapter 4, I quantified differences in range shifts and estimates of population viability at the northern range edge border based on outcomes of a correlative model (SDM) contrasted with a hybrid model that combined SDM outcomes with metapopulation dynamics models. A secondary objective was to evaluate the sensitivity of model outcomes using a global sensitivity analysis framework. Based on SDMs predictions, I found that the Hooded Warbler range was consistently projected to shift north: choice of GCMs influenced the magnitude of change, and variability was spatially structured. Variability in the choice of GCMs propagated through to metapopulation viability at the northern

range boundary. Consistent with a priori predictions, based on a hybrid modelling approach that combined SDMs with metapopulation dynamics models, viability measures were most sensitive to direct habitat loss. Despite the high ranking of vital rates in the global sensitivity analysis, direct habitat loss had a larger negative influence on extinction risk than potential future climate changes. This work underscores the importance of a global sensitivity analysis framework applied to hybrid models to disentangle the relative influence of uncertainties on projections. Key findings of this chapter include the significance of accounting for multiple and potentially opposing threats using demographic models to estimate rates of range expansion.

Migratory bird species present a unique challenge for conservation planning under climate change due to their complex life histories. In Chapter 5, while accounting for a range of model uncertainties, I quantified the sensitivity of spatial priorities under projected climate change to the inclusion of a habitat predictor variable in species distribution models across breeding and nonbreeding ranges of 28 Nearctic-Neotropical migratory bird species. The addition of a single biotic predictor, forested habitats, had cascading influences on the selection of spatial priority areas for conservation. Identification of climatically suitable priority areas achieved lower representation of forested habitats required for vegetation dependent species relative to biotic derived priorities, largely a result of elevated commission error rates. Spatial incongruence between abiotic (climate) and biotic (forest) SDM derived priorities were amplified when projected climate change was considered while the pattern of spatial priorities varied in asymmetric ways depending on the seasonal range under consideration. High latitude breeding priorities resulted in large northward shifts, while differences in nonbreeding priorities were characterized by more complex heterogeneous patterns.

6.2   General conclusions

In this thesis, I have shown that biotic vegetation factors are important determinants of species' distributions, alongside abiotic (i.e., climate) factors (Chapters 2, 3). The importance of biotic vegetation covariates is linked to the specific habitat requirements for the *Parulidae* warblers examined throughout this thesis. While abiotic (i.e. climatic) factors were on average ranked higher in permutation importance, the inclusion of biotic vegetation covariates tended to decrease errors of commission based on broad-scale correlative models, which had cascading consequences on both predicted range shifts under climate change and the development of spatial

conservation priorities robust to climate change. This underscores the importance of including ecologically relevant variables that represent resource availability and limiting factors of the focal species. However, the generality of the relative strength of abiotic relative to biotic factors is sensitive to temporal resolution and spatial scale. In particular, case studies using dynamic occupancy models and metapopulation dynamics models both suggest that direct habitat loss can have a stronger effect, at least at finer temporal scales. I have also shown that landscape level habitat management is needed for species that are expanding their ranges northward in particular at the northern boundary as the ability to track climate change is dependent in part on the availability of suitable biotic habitat elements (Chapter 4). As managers are required to make decisions quite often with imperfect knowledge, a particular novelty of Chapter 4 is the development of tool to automate sensitivity analyses of coupled SDM-PVA models that can be used to evaluate the consequences of different amounts of habitat loss on species' range expansion under different GCMs. There are an increasing number of studies that integrate biotic vegetation in addition to abiotic factors either for understanding determinants of current distributions or consequences of climate change (e.g., Barbet-Massin *et al.*, 2012b, Scott *et al.*, 2014). However, few model entire species' distributions (e.g., Cumming *et al.*, 2014) or they consider only a singular season (i.e. breeding and nonbreeding) thus capturing only a portion of the annual lifecycle of long-distance migratory species (but see Doswald *et al.*, 2009).

The finding that species distributions were influenced by short-term dynamic changes in habitat and extreme short-term climatic events represents an important advancement in the study of range dynamics (Chapter 3). To date, few studies consider the importance of fine temporal scale of climate and habitat changes, instead assuming that static spatial data is adequate to model species' distributions. Understanding the relative importance of factors limiting species' distributions, which in Chapter 3 represents threatening processes of habitat loss and climate change, can help to inform decision-making aimed at abating threats. My work suggests that species' are responding to short-term changes in both climate and habitat, however, changes in vegetation cover were more strongly associated with extinction risk. Despite the broad spatial scale of this study, this underscores habitat management in climatically favourable areas as a potential management strategy for the Near-Threatened Golden-Winged Warbler (IUCN, 2010). Models that do not account for finer-temporal scale dynamics in both habitat and climate are

likely to overestimate suitable habitats and species' responses to climate change, which has important implications for conservation priorities and management decisions.

Finally, I have demonstrated the need to explicitly consider multiple sources of uncertainty in the modeling of species range dynamics, in particular under future global change scenarios. Uncertainty in model selection, type of modeling algorithm applied, and choice of General Circulation Models resulted in large variation in SDM outcomes (Chapter 2). By contrast, global sensitivity analyses of coupled SDM-PVA models revealed the importance of both uncertainty in demographic rates and in patterns and amount of habitat loss had a disproportionate influence on species persistence and its propensity for range expansion under favourable climate changes (Chapter 4). Both of these outcomes demonstrate the need to systematically account for uncertainties, but the relative influence of multiple sources of uncertainty may differ depending on model approach. Adopting approaches such as the use of consensus methods where model predictions are combined based on a decision rule (e.g., average predictions across levels within a factor) are valuable for reducing variation associated with any one modeling method or with wide variability associated with future climate change projections. This may be of particular relevance when the objective of the modeling process is to inform decision-making (Araújo & New, 2007b). However, knowledge of the source variation in model outcomes is important for refining models and improving model accuracy be developing better models. For example, SDMs calibrated based on a combination of abiotic and biotic factors, the latter of which includes both proxies for habitat describing vegetation features and biotic interactions between species, generally result in improved prediction performance (Luoto *et al.*, 2007, Syphard & Franklin, 2009, Peers *et al.*, 2013). In these cases, improved predictive accuracy is a result of incorporating ecologically relevant information. Integration of biotic factors and interactions into models is of particular relevance in the context of global change, where species distributions and interactions are likely to be modified by relationships with climate (Wisz *et al.*, 2013).

6.3   Future directions

There are several lines of inquiry that may help to improve our understanding of the factors that drive species' range dynamics and the development of improved predictive models.

(1) Importance of temporal scale of threatening processes

While most studies consider the role of long-term average climate trends, many species' are likely responsive to shorter-term climate changes (i.e. weather). In particular, short-term climate variability and the frequency and intensity of extreme climate events may influence species' distributions both in the short and long-term, yet these are often overlooked (Vasseur *et al.*, 2014). More frequent and intense climate events, such as droughts and heat waves, can have both direct effects on species' demographic rates or local extinction via dispersal ability and indirect effects for example mediated by interspecific competition. Outstanding questions include: (1) are there time-lagged responses and does this depend on temporal resolution, and (2) do life-history traits explain the scale of time-lagged responses. Additional lines of inquiry include whether poor SDM transferability over time (Rapacciuolo *et al.*, 2012) results from selection of abiotic predictors at an inappropriate temporal resolution. Developing models that consider finer scale temporal dynamics and finer spatial resolution of dynamic threatening processes should provide more ecologically relevant predictions that are likely to be more appropriate for management actions (Potter *et al.*, 2013).

(2) Consequences of climate change on seasonal biotic interactions of long-distance migratory birds

During the non-breeding season, many Nearctic-Neotropical migratory bird species form mixed species flocks both with other migratory species and resident species endemic to the Neotropics, where competition is the hypothesized mechanism structuring community patterns of co-occurrences (Graves & Gotelli, 1993). Recent findings suggest a role for interspecific competition between tropical resident species that may limit range shifts under climate change (Jankowski *et al.*, 2010). Thermal tolerances may differ between migratory and resident tropical species, which may further amplify the consequences of climate change on these different groups of species individually and indirectly through biotic interactions. Although far from resolved, research suggests that tropical species may be disproportionately vulnerable to climate change in part related to relatively narrow thermal tolerance adaptations (Freeman & Class Freeman, 2014). Migratory birds may be less vulnerable to climate change occurring over the nonbreeding season relative to tropical residents. This may in part be related to migrants tending towards more flexible basal metabolic rates (BMRs) relative to resident tropical species (McNab, 2009, Şekercioğlu *et al.*, 2012). BMR measures the rate of energy expenditure and is considered important for temperature regulation, whereby a higher BMR suggests an ability to tolerate

physiologically wider thermal conditions. If and how biotic interactions play out in association with limiting environmental conditions and potentially differing degrees of thermal tolerances between both migratory and resident tropical species remains an important area of research. Additional methods that would complement empirical data collection along range limits include testing the hypothesis of niche similarity between resident and tropical species (Warren *et al.*, 2008) and estimation of niche filling as an approach to assess the importance of biotic interactions in structuring species' ranges (Skov & Svenning, 2004). Given the importance of seasonal carry-over effects on population dynamics for migratory birds (Norris & Taylor, 2006), a coordinated research agenda across seasonal ranges with multi-national support should increase both efficiency of data acquisition and effectiveness of conservation actions.

(3) Longitudinal demographic research

Integrative studies drawing from a diverse set of approaches, such as experimental manipulation and mechanistic models, will be important for elucidating factors and mechanisms that influence species responses to global change (Dawson *et al.*, 2011), however, the paucity of longitudinal data remains a formidable barrier. Research or monitoring programs designed to collect abundance and ideally demographic rates across various spatial positions (e.g., across latitudinal gradients) of species' ranges will provide vital information that will contribute to a more mechanistic understanding of the causes of range shifts (Pagel & Schurr, 2012, Schurr *et al.*, 2012). For example, long-term mark-recapture data sets can help explain causal role of weather on survival and fecundity estimates of populations, providing a more mechanistic understanding of species' responses to changing environments (Dybala *et al.*, 2013). The development of population models parameterized based on demographic rates in relation to climate can then be used to predict the consequences climate change (e.g., Barbraud *et al.*, 2011, Pomara *et al.*, 2014), thus providing critical information for species conservation and management decisions. Given the magnitude of resources to obtain such data, even simply including estimates of abundance are important: species might be moving into or out of habitat because of changes in population size, and this can further inform of the initial stages of range shift, which may be masked by using only presence-absence data (Maggini *et al.*, 2011, Virkkala & Lehikoinen, 2014).

(4) The importance of range-wide analyses

Multiple factors influence how populations respond to climate change including biotic interactions, strength and intensity of climate change, resource availability, and life-history traits. These factors may be spatially structured or directional thus resulting in variable patterns in the direction and magnitude of range shifts. Recent work suggests that the observed pattern of range shifts are more complex than the unidirectional (e.g., northward) shift that is often invoked (VanDerWal *et al.*, 2013, Lenoir & Svenning, 2014), thus estimating species' responses across the multiple geographic dimensions of their range (i.e., latitude, longitude, and elevation/depth) will provide a more coherent picture of the impact of climate change concomitant with other global drivers of change. Longitudinal datasets of species occurrences and abundances across species' ranges could be used to address whether patterns and rates of range shift at different range margins (e.g., leading and trailing edges) are consistent over time among species. As communities with no current analogs are expected under climate change (Williams & Jackson, 2007), tests of the role of climate versus habitat loss on community reshuffling, or even biotic homogenization will be increasingly important from both a theoretical community ecology and applied ecology perspectives (e.g., Davey *et al.*, 2013). Finally, in the burgeoning field of species' range dynamics there are a diversity of metrics used to quantify range shifts. These metrics describe different facets of range shifts, including range size, direction, magnitude, bioclimatic velocity, and community turnover (e.g., Diniz-Filho *et al.*, 2009, Potter & Hargrove, 2013, Watts *et al.*, 2013, Serra-Diaz *et al.*, 2014). Chapter 2 revealed that the most influential sources of uncertainty varied as a function of the metric of range change. The development of a framework to better understand the diversity of range shift metrics, their expected behaviours, a classification system, and their interpretation in the context of multiple sources uncertainties will be an important future contribution to the field of range dynamics.

6.4 Final remarks

This thesis provides an important contribution to our understanding of seasonal range determinants and potential future range shifts under climate change for a subset of the *Parulidae*. I have highlighted the relevance of moving past SDMs that incorporate only abiotic factors and the need to embrace approaches that reflect the dynamic responses of species to both changes in climate and habitat elements. Throughout I have emphasized the need to understand the impact of uncertainties stemming from multiple sources over the modeling process, which is of

particular importance when model outcomes are applied to inform decision-making processes. The incremental steps in knowledge advancement are evident here; my work serves as stepping stone that opens the door to further lines of inquiry. Understanding range dynamics and in particular the demographic consequences of global stressors of climate and habitat loss on species, is both a challenge and an opportunity. In an era characterized by rapid global changes resulting from human activities (Steffen *et al.*, 2007), such that we are said to be entering Earth's sixth wave of extinction (Chapin *et al.*, 2000), requires that we place an emphasis on science to inform conservation and management-based decision-making.

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