Flying towards improved species distribution models and vulnerability assessments of Canadian birds

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Submitted September 2022

A thesis submitted to McGill University in partial fulfillment of the requirements of the degree of a Master's of Science (M.Sc)

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Abstract

Climate change is set to impact biodiversity around the globe. In response, pole-wards range shifts are being observed ubiquitously, leading to range contraction for species already living at northern latitudes, such as birds breeding in northern Canada. Any pole-wards shift by these species, or from other species moving up from the south, will cause range contraction and increased extinction risk. Canadian birds are experiencing climate-driven change faster than anywhere else in the world, making it critical to understand the magnitude of change they will experience in the future. Species distribution models (SDMs) are the most commonly used tool to understand the incoming climate-driven changes. Inferring from associations between observational occurrences and environmental data, these models are used to predict potential species distribution with future climate scenarios. However, many different distribution models have been developed, each based on different assumptions and better suited for different types of data. The Canadian north is a particular challenge, as it has rapid climate change and very sparse distribution data. While most SDMs are based only on occurrence data, some new approaches combine occurrences with abundances from systematic survey data, which could be a solution to having reliable models in under-sampled regions. In addition to projected species range shifts, species traits are well-known to be correlates for extinction risk. Combining SDMs with traits could provide a framework for understanding a species ability to cope or adapt to climate-driven change as well as changes in habitat suitability and identify vulnerable species not currently deemed at-risk.

In this thesis, I first address the question of how to integrate climate-change projections into a trait vulnerability assessment (TVA) framework. This new framework evaluates how much climate change a species is experiencing (i.e., how much suitable habitat they are predicted to lose and gain), which is then combined with species-specific traits. Species traits represent sensitivity, exposure, and adaptive capacity to climate change. By incorporating both SDM and TVA, I assessed the overall vulnerability of the 471 birds breeding in Canada and highlighted 83 species not currently at-risk, but likely to become vulnerable in the future given their combined changing distributions and capacity to withstand these changes.

Secondly, I ask how different data types can be leveraged to address data-deficiencies when predicting species distributions. I test a recently developed method of combining abundance and occurrence data for waterfowl of the western boreal region of Canada, where both types of data are limited and biased in different ways. I compare four different types of data and approaches including: (1) abundance data from the Waterfowl Breeding Population and Habitat Survey (WBPHS), (2) occurrence data derived from abundance data from WBPHS, (3) occurrence data weighted by abundance, and (4) occurrence data from the Global Biodiversity Information Facility (GBIF). I find that the simple method of model integration (occurrence data weighted by abundances) produces better predictions than individual models. I also determine which models are most appropriate depending on species rarity.

Overall, I find that an improved understanding of extinction risk is possible even in the rapidly-changing under-studied Canadian north, but we must leverage all available information to have reliable predictions of species risk.

Résumé

Les changements climatiques auront un impact sur la biodiversité dans le monde entier. En réponse à ces changements, divers taxa se déplacent vers les pôles, entraînant une contraction de l'aire de répartition et un risque accru d'extinction pour les espèces vivant déjà à des latitudes nordiques, comme les oiseaux qui se reproduisant dans le nord du Canada. En plus de subir une contraction de leur aire de répartition, les oiseaux canadiens endurent les changements climatiques plus rapidement que partout ailleurs dans le monde. Il est donc essentiel de comprendre l'ampleur des changements auxquels ils seront confrontés. Les modèles de répartition des espèces (SDM) sont l'outil le plus couramment utilisé pour étudier la réponse des espèces face aux changements climatiques à venir. Déduisant des associations entre les occurrences observées et les données environnementales, ces modèles sont utilisés pour prévoir la répartition potentielle des espèces en fonction des futures conditions climatiques. De nombreux modèles de répartition ont été développés, chacun basé sur des hypothèses différentes et mieux adapté à différents types de données. Le nord du Canada représente un défi particulier car il connaît des changements climatiques rapides et des données de répartition très éparses. Alors que la plupart des SDMs sont basés uniquement sur des données d'occurrence, certaines nouvelles approches combinent les occurrences avec les abondances provenant de données d'enquêtes systématiques, ce qui pourrait être une solution pour avoir des modèles fiables dans les régions sous-échantillonnées. En plus des déplacements prévus des aires de répartition des espèces, les caractéristiques des espèces sont bien connues pour être des corrélats du risque d'extinction. La combinaison des SDMs avec les traits pourraient fournir un cadre pour comprendre la capacité d'une espèce à faire face ou à s'adapter aux changements climatiques ainsi qu'aux changements dans l'adéquation de l'habitat et identifier les espèces vulnérables qui ne sont pas actuellement considérées comme en danger.

Dans cette thèse, j'aborde la question de savoir comment intégrer les projections de changement climatique dans un cadre d'évaluation de la vulnérabilité des traits (TVA). Ce nouveau cadre évalue l'ampleur du changement climatique auquel une espèce est confrontée (c'est-à-dire la quantité d'habitat approprié qu'elle est censée perdre ou gagner), qui est ensuite combinée aux traits spécifiques de l'espèce. Les caractéristiques des espèces représentent la sensibilité, l'exposition et la capacité d'adaptation au changement climatique. En intégrant les SDMs et le TVA, j'ai évalué la vulnérabilité globale des 471 oiseaux qui nichent au Canada et j'ai mis en évidence 83 espèces qui ne sont pas actuellement en danger, mais qui seront probablement vulnérables à l'avenir compte tenu de l'évolution combinée de leur climat et de leur capacité à résister à ces changements.

Deuxièmement, je me demande comment les différents types de données peuvent être exploités pour remédier aux déficiences des données lors de la prévision de la répartition des espèces. Je teste une méthode récemment développée pour combiner les données d'abondance et d'occurrence des oiseaux aquatiques de la région boréale occidentale du Canada, où les deux types de données sont limités et préjugés de différentes manières. Je compare quatre types de données et d'approches différentes : (1) les données d'abondance provenant du *Waterfowl Breeding Population and Habitat Survey* (WBPHS), (2) les données d'occurrence dérivées des données d'abondance du WBPHS, (3) les données d'occurrence pondérées par l'abondance, et (4) les données d'occurrence provenant du *Global Biodiversity Information Facility* (GBIF). Je constate que la méthode simple d'intégration des modèles (données d'occurrence pondérées par

les abondances) produit de meilleures prédictions que les modèles individuels. Je détermine également quels modèles sont les plus appropriés en fonction de la rareté des espèces.

Dans l'ensemble, je constate qu'il est possible d'améliorer la compréhension du risque d'extinction, même dans le nord du Canada, qui évolue rapidement et qui est sous-étudié, mais nous devons exploiter toutes les informations disponibles pour obtenir des prévisions fiables sur le risque pour les espèces.

Acknowledgements

I would first like to thank my supervisor, Laura Pollock, for taking me on as a master's student. You have provided a wonderful environment to learn and grow both professionally and personally. You gave me great opportunities for me to learn, like internships, working groups, certifications, and a collaboration with Canadian Wildlife Services. I have learnt so much while working with you and have thoroughly enjoyed learning about quantitative biology and about life! I will always be grateful for your continued help and support throughout my thesis, and especially for answering my many many questions!

I would like to thank the examiner of my thesis, Virginie Millien, for taking the time to review and provide feedback. Your comments and feedback are truly appreciated and helped further improve my thesis.

Further, I would like to thank the members of my supervisory committee, Kyle Elliot, and Brian Leung, for your help in shaping my thesis. During our committee meetings you were both very helpful and supportive in regard to my work. Your feedback, opinions and encouragement were very appreciated, and I am grateful for all your help.

This thesis was also successful thanks to the data availability provided by the Global Biodiversity Information Facility (GBIF), as well as all the information available from IUCN Red List and Birds of the World by the Cornel Lab of Ornithology. Further thanks goes to the U.S. Fish and Wildlife Services for providing the Western Breeding and Population Habitat Survey data. I would also like to thank the Canadian Wildlife Services and Environment and Climate Change Canada, for allowing me to collaborate with them on parts of the Western Boreal Initiative project.

To my colleagues and friends in the Pollock lab, thank you for providing a great office environment full of support, encouragement, great ideas, and laughter! Thank you to my friend and colleague Jonathan Diamond for helping me throughout my master's and for reviewing and editing many drafts, R troubleshooting and answering my many questions.

Last but not least, I would like to say thank you to my family. My parents, Lynda Tanguay and David Brown, as well as my siblings, Kyle and Alyssa Brown, helped and encouraged me throughout my studies. Your constant encouragement and support through the hardest and most stressful parts of my academic career has been invaluable and I will forever be grateful. And to my best friend and amazing partner Daniel Miron, thank you for always being there for me. Thank you for always making me laugh and encouraging me, and especially for listening to me talk week after week about species distribution models, my struggles in R, my writers-block rants, and for listening to me practice every presentation I've had to give throughout my studies.

Contribution to original knowledge

This work was built upon previous work and research on trait vulnerability assessments (TVA) and species distribution models (SDMs). Here, I further developed a TVA framework to improve vulnerability assessments for biodiversity. Moreover, I aimed to improve model performance and predictive ability of SDMs by working with various types of data, as well as implementing a newly developed weighted technique for SDMs. The results derived from this thesis provide further knowledge on improving species distribution models and can be utilized for further research across different study systems and species. The frameworks and models developed here could also be used for conservation and wildlife management, spatial prioritization, and vulnerability assessments for less well-known species.

Contribution of Authors

Andrea Brown and Dr. Laura Pollock both devised the ideas presented here. With the help and supervision of Dr. Pollock, Andrea Brown lead the data curation and cleaning, methodology performed, formal analysis, and the writing of the original draft. Throughout all steps of this project Dr. Pollock actively provided expert knowledge and feedback as well as reviewed and edited drafts.

Introduction

Few areas in North America remain untouched by global climate change. From increases in frequency and severity in extreme temperatures, to decreased glacial extents and sea level rise, to increased heatwaves, climate change impacts are unavoidable, spanning terrestrial, freshwater, and marine systems (IPCC, 2022). Warming temperatures are impacting biodiversity in various ways, including changes in ecosystem structure, species range shifts, and changes in phenology (IPCC, 2022). However, such impacts are even more drastic at northern latitudes, particularly in Northern Canada. Northern Canada is the home and the breeding grounds for hundreds of birds but remains under-sampled, and understudied, despite being extremely vulnerable to climate change. Species distribution models (SDMs) have been developed to evaluate species exposure to climate change and are the primary tool used for such assessments (Elith and Leathwick, 2009; Willis et al., 2015). These models use associations between observational and environmental data to predict a species current and potential future distribution across a spatial and temporal landscape using various temperature and green house gas emission scenarios (Elith and Leathwick, 2009; Lawler et al., 2011). One major advantage of SDMs is that continuous maps of suitable habitat can be predicted at any spatial resolution with sufficient data. SDMs are used from detailed analyses of individual species to global predictions at coarse grid cells involving thousands of species. However, there are many biotic and abiotic factors that influence a species distribution which are not considered in SDMs. Most SDMs only assess the magnitude of predicted geographical shifts in habitat and climate suitability (Willis et al., 2015). While such information is still very useful, it lacks all the components needed to robustly assess climate change vulnerability as an SDM simply describes the changes in (modelled) suitable habitat, not the response of the species to such change.

To accurately assess vulnerability, other factors such as species traits, and changes in abundance, must be considered. First, using only SDMs for climate-change vulnerability assessments does not capture a species ability to cope and adapt with environmental change. SDMs generally only use bioclimatic variables (Elith and Leathwick, 2009) and much less commonly include species-specific traits. The resulting predicted distributions are, therefore, models of the realized niche of species as defined by climate variables. As the observed occurrences of many species are a subset of the fundamental (Soberón, 2007) or tolerance niche (Sax et al., 2013), then the models would likely under-predict the geographic area that the species could occur in given a particular set of circumstances (e.g. the absence of competitor species). If this is the case, then vulnerability estimates derived from an SDM might under-estimate climate change risk for a species (Bush et al., 2018). One way to better understand vulnerability to climate change is to use additional biological information about species (e.g., functional traits) to help refine predictions of change and estimates of vulnerability. Species-specific traits can increase or decrease a species vulnerability to climate change, and therefore, influence their extinction risk (Willis et al., 2015). For example, Ducatez et al., (2020) investigated how behavioural plasticity is associated with extinction risk in birds. They used innovation propensity (a species ability to develop a new behavioral response in the face of climate-driven change) as a measure of behavioural plasticity and found a negative relationship with extinction risk (Ducatez et al., 2020). Behavioural plasticity reflects a species ability to adapt to environmental change, therefore species with increased innovation ability have lower extinction risk and are more likely to have stable, or even increasing, population size (Ducatez et al., 2020). Combining life-history traits with SDMs can provide a more complete assessment of not only how much change in suitable habitat each species is experiencing, but also if they can adapt to such changes. For instance, SDM may find that a particular species is predicted to gain suitable habitat and life history-traits can determine if such species can disperse, survive, and reproduce in this newly available habitat (Willis et al., 2015).

Second, most SDMs use presence-only or presence-absence data, but many researchers argue that using abundance data (i.e., count data) is a better metric. While the collection of abundance data is more costly and resource demanding, it can provide more valuable models results. For example, Johnston et al., (2015) compared the conservation prioritization results between occurrence and abundance models for the Northern Pintail (*Anas acuta*) in California. Results from the occurrence model analysis highlights three regions in the Central Valley as important for the Northern Pintail, however the abundance model analysis highlighted all locations within one of the three regions in the Central Valley: the Sacramento River Valley, where 71-95% of the Northern Pintail population resides (Johnston et al., 2015). Abundance model outputs can also quantify the number of individuals in an area, and thus their impact of the local community, whereas presence-absence models simply state that at least one single individual is present (Elith and Leathwick, 2009; Martínez-Minaya et al., 2018). In theory, habitat suitability can be extrapolated based on abundance model outputs, but the abundance-suitability relationship has mixed support in the literature (Dallas and Hastings, 2018; Weber et al., 2017). Despite this, using abundance data can provide valuable baseline data, and can potentially provide early warning signs of population decline (Howard et al., 2015; Waldock et al., 2022; Yu et al., 2020). However, abundance models should be used with caution, as they may not be appropriate for all species.

In this thesis, I evaluate the vulnerability of Canadian birds to climate change. More specifically, I first combine SDMs and Trait Vulnerability Assessments (TVA) to develop an integrated approach that considers geographical shifts in suitable habitat, as well as each species ability to cope and adapt to such climate-driven change. Following this, I investigate the best approach to use when working with abundance data with SDMs, looking into how a species ecology may influence the model performance and therefore, model selection. These results can be used to better inform conservation management, spatial prioritization, and species-specific conservation. SDMs solely based on occurrence data can only provide so much information on a species vulnerability to climate change. Additional information, such as life history traits, biotic and abiotic interactions, home range size and changes in abundance, is needed to produce more accurate and informative results for conservation purposes. For the purpose of this thesis, I will focus on how incorporating life history traits and abundance data with SDMs will influence model performance and outputs.

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Integrating species distribution models with trait vulnerability assessments for Canadian birds

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Abstract

Aim: Species distributions models (SDMs) are the most widely used tool to determine climate change impacts on biodiversity. However, SDMs only consider environmental change, and do not consider a species ability to adjust and handle with these changes. Biological traits provide a wealth of information on how well a species can cope with climate-driven change. Here, we aim to combine more explicitly SDM predictions into each TVA component, to provide a vulnerability assessment which considers both extrinsic changes and intrinsic ability of each species.

Location: Canada

Methods: SDMs were produced for all 471 species of birds breeding in Canada. From these predictions, the amount of habitat gained and lost by each species is used as a trait to reflect their expected geographical change in suitable habitat. The expected geographical change in suitable habitat was then incorporated into each TVA component with other biological traits which reflect a species sensitivity, adaptive capacity, and exposure to climate change. The vulnerability risk for all 471 species was assessed across life history guilds and breeding biomes.

Main Conclusion: This assessment highlights seabirds, shorebirds, waterfowl, and wetland birds to be the most vulnerable to climate change, with each group having high vulnerability scores in at least one of the TVA components. We identified 83 species most likely to become vulnerable with increased climate-driven change, most of which breed in the Artic Tundra, wetlands, and coastal habitats. Finally, we show that northern species are more vulnerable to climate change due to both their biological traits and their predicted change in suitable habitat. Incorporating SDMs with TVAs can provide information about how a species' habitat availability will be altered due to climate change as well as help determine if they can persist in decreasing habitat or disperse to new available habitat.

Key words: *adaptive capacity, Aves, climate change, exposure, sensitivity, species distribution models, trait vulnerability assessment*

Introduction

Climate change is set to impact birds around world, but northern species are particularly vulnerable and under studied (Bellard et al., 2012; Nixon et al., 2016; Gaudreau et al., 2018). To prevent losses, species will need to adapt to new environmental conditions or disperse to follow their climate niche (Bateman et al., 2020), with the latter already observed in many taxa shifting their range pole-wards (Walther et al., 2002). However, for birds already at the physical limits of their habitat, such as Arctic breeding birds, any northward shift will cause range contractions, reducing their breeding habitat and increasing their extinction risk. Already 24-50% of bird species globally are vulnerable to climate change (Foden et al., 2013), and many more species are expected to experience a decrease in range size globally (Walter et al., 2007). Range shifts and changes in climate conditions can cause changes in migration timing (arriving early or late on the breeding grounds), potentially eliciting a mismatch between nutrient availability and nutrient demand for migratory birds, and thus impacting population size and species survivorship (Smith et al., 2020). In addition to changes in range size, species-specific traits can also impact vulnerability status. Species with traits that promote specialist behavior are more likely to be vulnerable to climate change compared to generalist species (Chichorro et al., 2019). With Canada warming more than two times faster than the rest of the world, and the Arctic is warming three times faster (Bush and Lemmen, 2019), identifying species in need of protection is vital for their survival. We urgently need to evaluate comprehensive risk for northern species which are likely to become more vulnerable with rapid climate change.

To evaluate risk, we need to determine if a species is vulnerable because of their traits, making them unable to persist or disperse, or from climate change driven habitat loss, or both. Species distribution models (SDMs) are the most widely used tool for predicting climate change impacts on biodiversity and assessing changes in range size at both a regional (Brian et al., 2008) and local scale (Berteaux et al., 2010; Gaudreau et al., 2018). However, SDMs use bioclimatic variables to project species distribution with future changes in habitat without including their ability to cope with these changes (Willis et al., 2015). Other issues with SDMs include weak relationship between extinction risk and predicted changes in habitat suitability (Fordham et al., 2012), spatial and temporal autocorrelation (Martínez-Minaya et al., 2018; Miller, 2012), non-stationarity (which reflect spatial heterogeneity; Martínez-Minaya et al., 2018; Miller, 2012), sampling bias (Martínez-Minaya et al., 2018), etc. If SDMs incorrectly assume an environmental variable represents a fundamental limit for a species, then projected range losses could be over-estimated as the species might not actually need to move to track the climate. On the other hand, since SDMs do not consider a species' persistence or dispersal ability, models may over-estimate predicted range availability and under-estimate the vulnerability risk. For example, SDMs predicted a 600% increase in current distribution size for the White-necked Picathartes (*Picathartes gymnocephalus*), however their low dispersal ability makes them unlikely to colonize the newly available habitat (Willis et al., 2015). In this case, SDMs over-estimated potential range availability and under-estimated vulnerability risk, when in fact, the low dispersal ability of the White-necked Picathartes, combined with a 50% loss of its current range, makes it highly vulnerable to climate change (Willis et al., 2015). In practice, SDMs have mixed results when projecting past range shifts of species (Sofaer et al., 2018), although they might become more predictive as climate change causes major shifts. Despite this, SDMs remain useful, and in many cases, the only tool for understanding potential climate change impacts for a species. But SDMs should be combined with additional information for each species rather than used in isolation to predict the impact of climate change. Not considering biological traits could result in

(1) an under-assessment of vulnerability status derived from models which do not consider intrinsic ability to cope with modelled geographical change, and (2) increased extinction risk due to reduced or absent conservation management developed based on inaccurate modelling results.

The other source of information readily available for all species is biological traits. Traits form the basis for trait vulnerability assessments (TVA), which evaluate vulnerability based on intrinsic abilities and extrinsic opportunity (Willis et al., 2015). For example, habitat specialization is a trait commonly used to reflect a species sensitivity, such that specialists are more sensitive to climate change due to their narrow habitat requirements compared to generalist (Foden et al., 2013; Gardali et al., 2012). TVA's combine species exposure to climate change and species-specific characteristics to determine their vulnerability status and assess if particular traits increase or decrease their vulnerability (Willis et al., 2015). Many climate change vulnerability assessments have been developed over the years (Barrows et al., 2014; Foden et al., 2013; Gardali et al., 2012; Garnett et al., 2013; Triviño et al., 2013; Young et al., 2012) all using traits to describe the same three components for each species: sensitivity, adaptive capacity, and exposure to climate change (Wheatley et al., 2017). However, the methodologies and the traits used to estimate each component of these assessments varies from framework to framework, with little to no consistency (Wheatley et al., 2017). One study compared the outputs of 12 different vulnerability assessment frameworks, including trait- and trend-based (which focus more on changes in abundance and distribution, rather than traits) approaches, to determine if they generate similar findings (Wheatley et al., 2017). Each framework provided differing results, with none of them assigning the same risk category for a single species (Wheatley et al., 2017), suggesting the inconsistencies are a product of the variables used and how they are combined rather than from the data used in each assessment.

Despite SDM predictions being one of the only tools for predicting climate change impacts across many species, few studies have incorporated SDM predictions into vulnerability assessments. In an early example, Foden et al., (2013) included projected changes in temperature and precipitation from SDMs for birds into their calculation of exposure and included five “trait sets” for sensitivity and two for adaptive capacity (Foden et al., 2013). Bateman et al., (2020) includes more details from the SDM projections in the TVA by partitioning projections into habitat gained, lost, and maintained. They then merge traits with SDM projections by including dispersal ability in the adaptive capacity component of their TVA to reflect a species ability to realize these predicted gains and also use SDM predictions for exposure (the climate change scenario considered) and sensitivity (range loss due to climate change; Bateman et al., 2020).

Here, we build upon the Bateman et al. approach by expanding the SDM-trait links in a TVA. We similarly partition SDM projections into area that is lost, potentially gained, and maintained (‘win-win’ areas projected to be stable into the future). We then combine those partitions with trait information that indicates how well species could track their climate niche (adaptive capacity) as well as traits that enable a species to persist in those areas of rapidly changing climate (sensitivity). We also include other threats in addition to climate change in our estimate of exposure and use a probabilistic approach to estimate habitat gained and lost for each species. We develop this TVA for breeding birds of Canada (471 species), which are highly exposed to rapid climate change and where we have detailed information of species traits and threats. Our results include a ranked list of the vulnerability scores of all species. By comparing vulnerability scores to their IUCN status, we identify currently overlooked species that are most likely to become vulnerable in the future. Finally, we compared TVA results to current trends in species abundance to highlight traits potentially related to declines in abundance, causing increased vulnerability in the near future.

Methods

Occurrence data - Occurrence data for 471 species of birds breeding in Canada was downloaded from Global Biodiversity Informatics Facility (GBIF: gbif.org) and filtered to extract breeding range data only. Only records later than 2000 were kept to avoid localities with large spatial uncertainties or those that might have shifted their ranges. The average start and end date of the breeding season was estimated for a random subsample of species (n = 117; 25% of species), generating a breeding season from June to July (similar breeding period as in Bateman et al. (2020); eBird, 2017; Bateman et al., 2020; Fink et al., 2020). For species that didn't have dates associated with their occurrence records, we included occurrence points only when they were within the IUCN breeding polygons when available (IUCN, 2021). When breeding polygons were not available, we used one of two approaches (Fig. S1). We first determined if the distribution data was within the general breeding range of that species (based on distribution maps from Birds of the World; Birds of the World, 2020). If the data was distributed similarly to the breeding range, only obvious outliers were excluded. If the occurrence data was distributed across North America and removing outliers was not an option, we used manually drawn breeding ranges. The manually drawn breeding ranges were approximations of the breeding range of each of the remaining birds (3%; Fig. 1). Distribution maps from Birds of the World (Birds of the World, 2020) were used as a reference for range extent, which was then used to exclude all points outside of these polygons. Occurrence data was then gridded for a 1-km^2 grid on a Lambert Conformal Conic projection.

Climate and environmental variables - We used current and future climate variables generated by AdaptWest (AdaptWest Project 2021) and non-climate habitat variables from a range of sources for our SDMs for the same grid as distribution data (1-km^2). Five climatic variables were included which were previously found to be important for modelling species distributions in breeding ranges (Bateman *et al.*, 2020; Wilsey *et al.*, 2019), and three topographic variables (Table S1). Future climate predictions included downscaled data from the Coupled Model Intercomparison Project phase 6 (CMIP6) in accordance with the 6th IPCC Assessment Report, as well as current data from PRISM and WorldClim. Future projections consist of an ensemble projection from 13 CMIP5 models (ACCESS-ESM1-5, BCC-CSM2-MR, CNRM-ESM2-1, CanESM5, EC-Earth3, GFDL-ESM4, GISS-E2-1-G, INM-CM5-0, IPSL-CM6A-LR, MIROC6, MPI-ESM1-2-HR, MRI-ESM2-0, UKESM1-0-LL). Current climate variables consisted of climate normal data from 1991 to 2020. We used emissions scenario 8.5 Representative Concentration Pathway 6 (RCP6) and projections for 2080. While emissions scenario 8.5 produces more changes in projected distributions (Thuiller et al., 2019) than mid-range scenarios, in this paper we wanted to assess the potential for future vulnerability under these strong, but not necessarily unrealistic scenario. RCP8.5 emphasizes high population growth, slow income growth, and modest rates of technological development with no climate change policies (Riahi et al., 2011; van Vuuren et al., 2011). By using this worst case - high emission scenario we can forecast the most drastic changes in species distribution and use these predictions to implement mitigation and conservation measures.

Species Distribution models – Three separate distribution models were used for each species: Generalized Additive Model (GAM), Boosted Regression Tree (BRT), and Maximum Entropy (MaxEnt) model. These models have been found to have high performance when being compared to other distribution models (Eskildsen et al., 2013). Models were built using the *mgcv*, *gbm*, and *dismo* packages in R (R Core Team, 2020). Models were fitted on data from the United States and Canada to avoid truncating environmental variables, and predictions were made only for Canada at a 5-km^2 grid scale. We then averaged across this set of models to produce an ensemble prediction for each grid cell for current and future predictions. From these model layers, we then calculated for species i, plot j, cells that were gained (occur in the future but not in the present), lost (occur in the present but not the future), and remained stable (occur in the present and the future). A gain for species i in cell j was calculated as the probability of occurrence in the future (F_{ij}) subtracted by the probability of occurrence in the present (P_{ij}) for each cell (F_{ij} - P_{ij}). Conversely, a loss for species i in cell j was calculated as the probability of occurrence in the present subtracted by the probability of occurrence in the future (P_{ij} - F_{ij}) for each cell. The number of cells that remained stable for species i in cell j was calculated as the sum of the probability of occurrence in the present and the probability of occurrence in the future, divided by two ($(F_{ij} + P_{ij})/2$). We validated SDMs based on suitability within their known breeding range (IUCN boundary plus a 500 km buffer) rather than the typical approach for pseudo-absence data, where zero are drawn from within and outside the known range. We used this approach because we wanted a realistic range extent, therefore we clipped predictions to the same buffered breeding boundary to synchronise the validations within the same extent. Validation of SDMs was done using two metrics across all of Canada: Area under the receiving operator curve (AUC) and area under the precision-recall curve (AU-PRC). AU-PRC in particular, does not incorporate the correct predictions of absences into its calculation, therefor increasing the geographical extent or including highly unsuitable locations in the model does not influence AU-PRC, making it ideal for less common and rare species (Sofaer et al., 2019; Vesk et al., 2021).

Trait vulnerability assessment (TVA) – We compiled a biological traits dataset for all 471 species breeding in Canada. Various morphological and biological traits were collected from a range of sources. Once all available trait data was assembled, we imputed 50 missing trait values using the *missForest* package in R. Using this dataset, traits that reflected a species sensitivity, adaptive capacity, and exposure to climate change were extracted (Table S1; Bateman et al., 2020; Foden et al., 2013; Gardali et al., 2012; Ofori et al., 2017; Willis et al., 2015).

Sensitivity reflects intrinsic traits that make a species vulnerable to climate change and unable to persevere (Foden et al., 2013; Gardali et al., 2012). We considered sensitivity to be comprised of (1) a species ability to persist in their environment, and (2) the amount of suitable habitat they are predicted to lose relative to their current distribution. Three traits were used to estimate persistence ability. First, the number of strata a species forages in was used to reflect either generalist or specialist behaviour, where specialists would have a lower persistence ability due to their narrow resource requirements. Second, innovativeness is a measure of behavioural plasticity, which reflects a species ability to develop new foraging techniques or affinities for new food resources as their available habitat changes (Ducatez et al., 2020). Third, generation length reflects how quickly a species can reproduce and evolve to new environmental conditions. Persistence traits were normalized (where greater persistence values indicate lower persistence ability) and summed to estimate persistence ability. Persistence and relative loss of suitable habitat were then summed to obtain sensitivity (Fig. 1A, Fig. 1B).

Adaptive capacity reflects a species ability to adjust to the effects of climate change, which includes their ability to disperse and colonize newly available habitats (Foden et al., 2019; Gardali et al., 2012). Here, we considered adaptive capacity to be comprised of two components, (1) a species ability to disperse, and (2) the amount of suitable habitat they are predicted to gain due to climate change. We used three traits to reflect dispersal ability. First, the number of habitats a species is found in was used to reflect either a generalist or specialist behaviour such that generalist will have greater potential to disperse and colonize new habitats compared to specialists. Second, clutch size was used as a proxy for a species ability to adjust to environmental change, such that a larger clutch size would provide greater opportunity to adjust to environmental change as a species. Third, migration index would reflect a species physical ability to disperse long distances and disperse to newly available habitats. Dispersal traits were normalized (such that a greater dispersal value represents better dispersal ability) and summed to estimate dispersal ability. Dispersal ability and gain in suitable habitat were summed to obtain adaptive capacity (Fig. 1A, Fig. 1B).

Finally, exposure reflects the nature, magnitude, and rate of environmental and climatic pressures a species may experience based on their geographic location (Foden et al., 2019, 2013). Here, we normalized the number of threats a species has listed by IUCN and the net loss in suitable habitat, which were summed to calculate a species exposure to climate change (Fig. 1C).

The final TVA score was calculated using the following:

$$TVA = Exposure + Sensitivity - Adaptive\ Capacity \qquad \text{(Equation. 1)}$$

We calculated the average TVA score for each avian guild (a group of species with similar life history traits) and the average TVA score for currently at-risk (i.e., species listed as vulnerable, near threatened, endangered or critically endangered by IUCN). The TVA score of at-risk species was then used to identify species with greater TVA scores, which we identified as impending at-risk species, i.e. species most likely to become at-risk in the future. Finally, the current distribution of currently and impeding at-risk species was mapped across Canada to determine if any special patterns between the two groups could be observed.

Statistical Analyses – To compare the current IUCN status with the calculated TVA score, as well as with the three TVA components, two separate generalized linear models (GLM) were used (*binomial* family with a *logit* link). We also used two separate linear models (LM) to compare the TVA score, and TVA component scores for impending at-risk species. Further, we performed three separate linear models (LM) to investigate the relatedness between change in species abundance (Rosenberg *et al.*, 2019) and the SDM predictions, TVA scores, and TVA components.

Results

The validation metrics for across Canada produced a mean AUC of x̄ = 0.81 and AUPRC of x̄ = 0.73 (Fig. S3). SDMs performed best for shorebirds when using the AUC metric (x̄ = 0.84), whereas aerial insectivores performed best when using AUPRC (x̄ = 0.78).

Adaptive Capacity, Sensitivity and Exposure – Trait vulnerability scores consist of three components: sensitivity, adaptive capacity, and exposure to climate change. For sensitivity and adaptive capacity, we classified 471 species into four vulnerability categories; (1) low vulnerability, (2) climate vulnerable, (3) trait vulnerable, or (4) climate and trait vulnerability. For sensitivity, 7% of species identified as climate and trait vulnerable, meaning they will experience large habitat losses due to climate change in addition to low persistence potential within their habitat (Fig. 1B, Fig 2A). Of the remaining species, 4% are climate vulnerable and

63% are trait vulnerable, with the last 26% of species experiencing low vulnerability (they have high persistence potential in their environment and experience low loss in suitable habitat; Fig. 2A). For adaptive capacity, 47% of species are both climate and trait vulnerable, meaning they gained little to no suitable habitat caused by climate change and have low dispersal ability to access newly available habitats (Fig. 1B, Fig. 2B). Other species are vulnerable based either on climate (34%) or traits (9%), whereas 10% of species have low vulnerability (they have high persistence ability to new conditions and have new opportunities with climate change). For exposure, we classified species into three levels based on the number of threats that they are exposed to (i.e., threats other than climate change and sever weather). Most species experienced low exposure to climate change (64%), whereas 32% of species experienced moderate exposure and 3% experienced high exposure to climate change (Fig. 1C, Fig. 2C).

Trait vulnerability scores for avian guilds – Overall, seabirds had the highest average trait vulnerability score (mean score value ± s.d. here and after; $\bar{x} = 0.93 \pm 0.48$), but some species from all guilds were vulnerable (Fig. 3A). The contribution of each category to total trait vulnerability scores also varied between guilds, with some groups, such as shorebirds, which had the highest exposure ($\bar{x} = 0.68 \pm 0.34$), whereas others had the highest sensitivity (waterfowl ($\bar{x} = 0.93 \pm 0.29$) and wetland birds ($\bar{x} = 0.91 \pm 0.25$)) or lowest adaptive capacity (seabirds ($\bar{x} = 0.50 \pm 0.14$)). Eighty-three species had TVA scores greater than the TVA scores of currently at-risk species ($\bar{x} = 1.09$; Fig. 3B, 3C, Table 1, S1). These species were identified as impending at-risk species and had significantly higher exposure ($P < 2e\text{-}16$), higher sensitivity ($P = 3.04e\text{-}07$), lower adaptive capacity ($P = 1.57e\text{-}10$; Fig. 3B) and higher overall TVA scores ($P < 2e\text{-}16$; Fig. 3C), where alpha = 0.05. Furthermore, all breeding biomes host impending at-risk species however, most of these species (57%) breed in the Arctic Tundra (n = 16), wetlands (n = 12), and along coasts (n = 19; Fig. 3D).

Spatial distribution of vulnerable species – We mapped the distribution of both currently and impending at-risk species (Fig. 4, top). Both maps display a higher concentration of at-risk species in northern Canada, with the impending at-risk map displaying a much more drastic pattern compared to the currently at-risk species, suggesting increased number of at-risk species in northern Canada in the future. Further, we mapped the average TVA score for all species present within a cell, such that the TVA score is weighted by the probability of a presences. This map demonstrates areas in northern Canada having a higher average TVA, implying a higher vulnerability risk to climate change for species in the Arctic (Fig. 4).

Relationship with change in species abundance – The SDM predictions (net change in suitable habitat) and sensitivity were positively related to the change in species abundance ($P = 0.0038$, $P = 0.013$, respectively), so species with increasing sensitivity and projected habitat availability into the future (2080, from SDMs) have also already generally increased in abundance (documented from counts 1970-2017). The TVA score ($P = 0.033$), exposure ($P = 3.69e\text{-}08$) and adaptive capacity score ($P = 0.038$) were negatively related to change in species abundance (Table 3), so species with documented declines over the past decades generally had higher TVA and exposure scores as well as lower adaptive capacity in this analysis.

Discussion

Climate-driven change has onset the 6th major mass extinction, which is likely to have widespread impacts globally, but especially at northern latitudes. Establishing the vulnerability of species to climate change is key for effective and targeted conservation actions. By combining SDM predictions with trait vulnerability assessments, we aimed to better understand how and why some species are vulnerable to climate change while others are not, in addition to identifying species that may need protection sooner than anticipated. Our results indicate: (1) four avian guilds are particularly vulnerable to climate change, with 83 species newly identified as impending at-risk species; (2) impending at-risk species are disproportionately found in three habitats, with more than half of species breeding in the Arctic tundra, wetlands, and coastal habitats; and (3) SDM predictions, TVA scores and each TVA components are significantly related to change in species abundance.

Vulnerable avian guilds – Four guilds in particular were found to have the highest vulnerability to climate change: seabirds, shorebirds, waterfowl, and wetland birds. Seabirds had the highest overall TVA score and lowest adaptive capacity. Species of this guild occupy and breed in a unique, but also vulnerable habitat (coastline). Their narrow habitat and foraging requirements, combined with a net loss of almost 40% of suitable breeding habitat, are most likely strong factors influencing their high vulnerability score. Further, seabirds had the lowest adaptive capacity among avian guilds. Adaptive capacity reflects a species ability to adapt to new environments based on their dispersal ability, which is estimated from migration traits, number of habitats, and clutch size. Their narrow habitat requirements reduce the amount of potentially available habitat they could gain in the future, which increases their extinction risk. Further, seabirds have delayed sexual maturity and small clutch size, both of which have been associated with increased extinction risk (Grémillet and Boulinier, 2009, Clavel et al., 2011). Similar traits have been found to also be associated with threatened seabird species in previous research (Richards et al., 2021). Additionally, seabirds display high social resilience and reluctance to change breeding site (Grémillet and Boulinier, 2009) which likely increases their susceptibility to abrupt environmental changes.

The TVA further revealed that waterfowl and wetland birds have the highest sensitivity. Waterfowl and wetland birds were once severely endangered, with some species on the brink of extinction (North American Bird Conservation Initiative Canada, 2019). While these waterbirds have greatly increased in population abundance thanks to protection and restoration of key habitats and active hunting management (Rosenberg et al., 2019), they remain highly sensitive to climate change. Sensitivity reflects a species ability to persist under environmental change, here persistence is estimated from foraging habitat diversity, clutch size, and innovativeness. Both groups displayed low innovativeness, meaning they have little ability to develop new foraging techniques or use novel food resources (Ducatez et al., 2020). Additionally, these species are limited to foraging in-and-around the water, foraging primarily on seeds, vegetations, and invertebrates (Stafford et al., 2014). Both traits reflect specialist behaviour, which is associated with higher extinction risk (Chichorro et al., 2019; Ducatez et al., 2020). Although waterfowl and wetlands species have increased in abundance in recent years, their high sensitivity scores provide evidence that these birds may struggle to persist with increased climatic changes. Lastly, shorebirds had the highest exposure to climate change. In Canada, shorebirds are of particular conservation concern due to their severe population declines (Hope et al., 2019). These birds have narrow habitat requirements, relying primarily on the Arctic tundra and wetlands for breeding and foraging. Their reliance on these two endangered habitats increases their extinction risk (Bateman et al., 2020; Chichorro et al., 2019; Gilg et al., 2012) and is presumably the driving force of their high exposure to climate change, in addition to a predicted net loss of almost 50 % in suitable breeding habitats.

Seeing that this framework successfully highlighted avian guilds already known to be highly vulnerable climate change, we argue that it could also be used to investigate other avian guilds not currently under threat to determine their vulnerability based on the biological traits we used here. Further, we identified 83 impending at-risk species which have higher TVA scores than currently at-risk species. These impending at-risk species are species most likely to become vulnerable as climate change impacts continue to intensify, based on the combination of their biological traits and the severity of climate-driven change they are predicted to experience (Table S2).

Vulnerable Canadian habitats – More then half of impending at-rick species breed in three biomes: the Arctic tundra, wetlands, and coastal habitats. All three of these biomes are endangered due to climate-driven change. In the Artic tundra and wetlands, warming temperatures promote earlier appearance of flowering plants and invertebrates (Post et al., 2009; Drever et al., 2012). While this may seem advantageous for breeding birds it causes a mismatch in the timing of peak nutrient demand and the availability in abundant resource for breeding birds, eliciting impaired chick growth and increased mortality (Post et al., 2009; Smith et al., 2020). Further, the Arctic tundra and coastal habitats are experiencing similar phenomena called arctic or coastal squeeze. Northward shift in suitable breeding habitat will cause many Arctic birds to experience range contraction, with some species experiencing an “arctic squeeze”, as their northward range shifts become restricted by the Arctic coastline (Post et al., 2009; Smith et al., 2020; Wauchope et al., 2017). To a similar effect, many coastal habitats will experience a “coastal squeeze” as rises in sea level force coastal habitats to retreat inland (Jones et al., 2013). Some habitats will be constrained by human developments, such as cities, which will increase inundation risks along the coast, reducing breeding and foraging habitat availability for many birds (Von Holle et al., 2019).

Based on the similar spatial patterns between currently and impending at-risk species, we observe a higher concentration of at-risk species in northern Canada compared to the south (Fig. 4). Using our SDM integrated TVA framework, we provide further evidence that northern species are more vulnerable to climate change, which is consistent with findings and spatial distributions produced by Bateman et al., (2020). Further, we observe some highlighted areas in northern Canada which have a higher average TVA score, indicating that species currently present in these areas have increased vulnerability to climate change (Fig. 4). We also highlighted three major habitats that are highly important for impending at-risk species and are already known to be sensitive to climate change, supporting the efficacy of this framework.

Changes in species abundance – Previous work focused primarily on predicting species distribution in response to climate change, however predicting abundance is considered a better measure of the impacts these species have on its local community (Ehrlén and Morris, 2015). Here, the SDM predictions, overall TVA score and each TVA component were significantly related to change in species abundance. However, these results must be considered carefully. Few trait vulnerability assessments have tested their predictive power for change in species abundance (Wheatley et al., 2017). Strong relatedness between change in abundance and SDM predictions and TVA components does not translate to high predictability of change in abundance. Additionally, it is unlikely that climate change impacts are reflected in current abundance trends, but this may soon change. Further research into the relationship between these variables is needed to see how results from SDMs and TVAs can be used to predict change in abundance.

The avian guilds and biomes highlighted here are consistent with the current vulnerable and endangered status associated with both of these groups. Traits that result in high sensitivity, low adaptive capacity, and high exposure should be targeted for conservation efforts to increase species ability to persist or disperse with environmental changes. Global biodiversity is under threat from climate change; however, researchers and conservation practitioners cannot solely rely on SDMs to assess the potential global impacts. Additional information, such as biological traits, are needed to develop effective conservation management for species who will most likely become vulnerable in the near future.

Figures

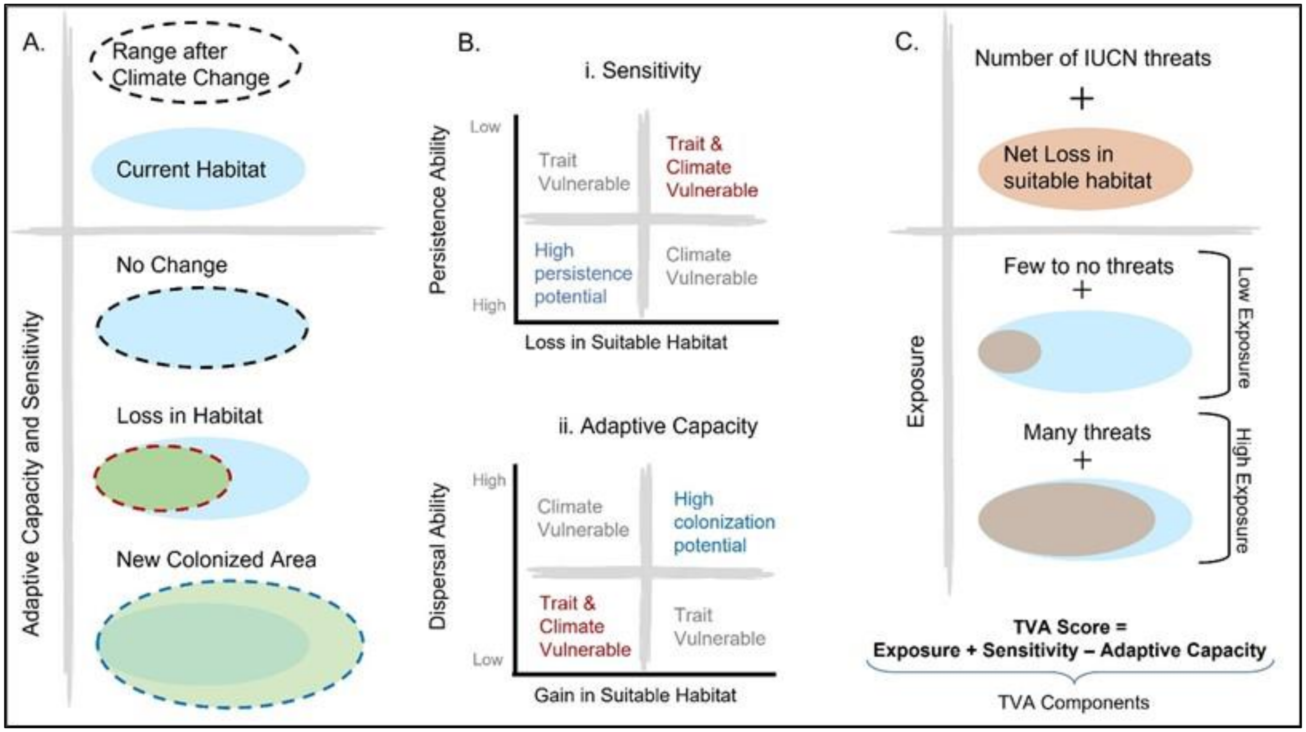

Figure 1. Conceptual diagram of how adaptive capacity, sensitivity and exposure are calculated using functional traits and SDM predictions. **A.** Potential change in species range after climate change. **B.** Relationship between functional traits and SDMs predictions used to estimate sensitivity (*i*) and adaptive capacity (*ii*). For sensitivity, if a species has a high persistence ability with little to no habitat loss (bottom left quadrant of *i*), then it has low sensitivity and low vulnerability to climate change. In contrast, if a species has low persistence ability with large habitat loss (top right quadrant of *i*), then it is highly sensitive to climate change seeing as it is unable to adjust to a changing environment and is experiencing high range contraction. In the case of adaptive capacity, if a species has a higher dispersal ability and new opportunities for colonization (a large gain in suitable habitat), then it has a greater adaptive capacity (upper right quadrant of *ii*). In contrast, if it has low dispersal capability and no new colonization opportunities (lower adaptive capacity) then it is more vulnerable (bottom left quadrant of *ii*). **C.** Exposure is calculated by summing the net loss in suitable habitat and the number of IUCN threats listed for each species. High net loss in suitable habitat with multiple IUCN threats increases exposure, whereas low net loss in suitable habitat and small number of IUCN threats decreases exposure.

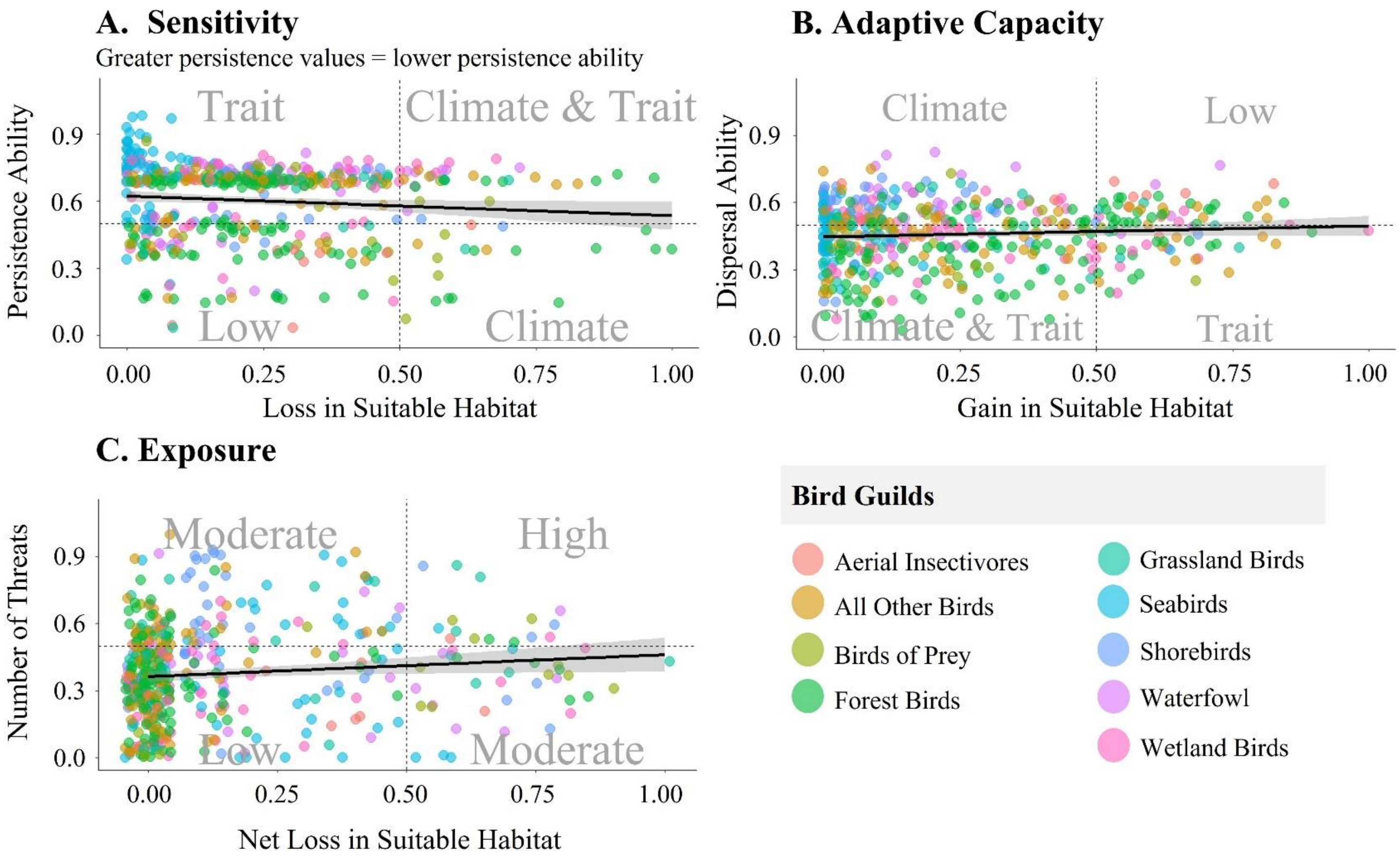

Figure 2. Trait vulnerability related to sensitivity (**A.**), adaptive capacity (**B.**), and exposure (**C.**) for each avian guild. Sensitivity is the combination of a species persistence ability (sum of number of foraging strata, total innovations, and generation length) and relative loss in suitable habitat. Adaptive capacity is a combination of a species ability to disperse (sum of migration traits, clutch size, and number of habitats) and gain in suitable breeding habitat. Exposure is the sum of the number of threats a species has according to IUCN RedList (excluding climate change and sever weather) and the net loss in suitable habitat.

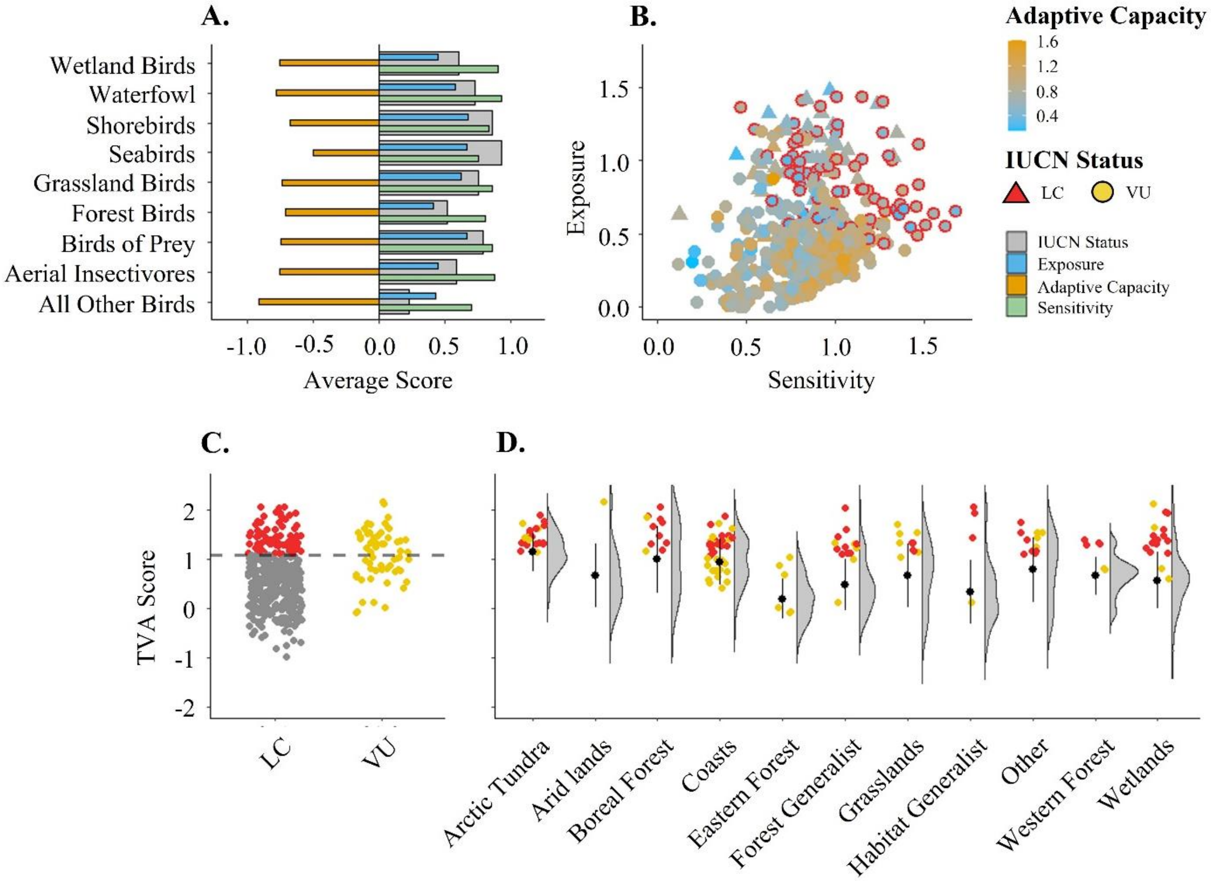

Figure 3. Breakdown of the TVA scores, and its components, across avian guilds, individuals, IUCN status, and breeding biomes. Impending at-risk species are species which are currently listed as Least Concern and have a TVA score greater then 1.09, shown as points circled in red (B.) or red points (C., D.), and species currently listed as Vulnerable are shown as yellow points (C., D.). **A.** TVA, sensitivity, adaptive capacity, and exposure scores for each avian guild, where TVA Index = Exposure + Sensitivity – Adaptive Capacity. **B.** The average scores for each TVA component. **C.** TVA scores for species currently listed as Least Concern (LC), and as Vulnerable (VU). VU included species listed Vulnerable, Near Threatened, Endangered, and Critically Endangered. The mean TVA score for Vulnerable species is shown by the black dashed line ($\bar{x}$ = 1.09). **D.** The distribution of TVA scores within each breeding biome.

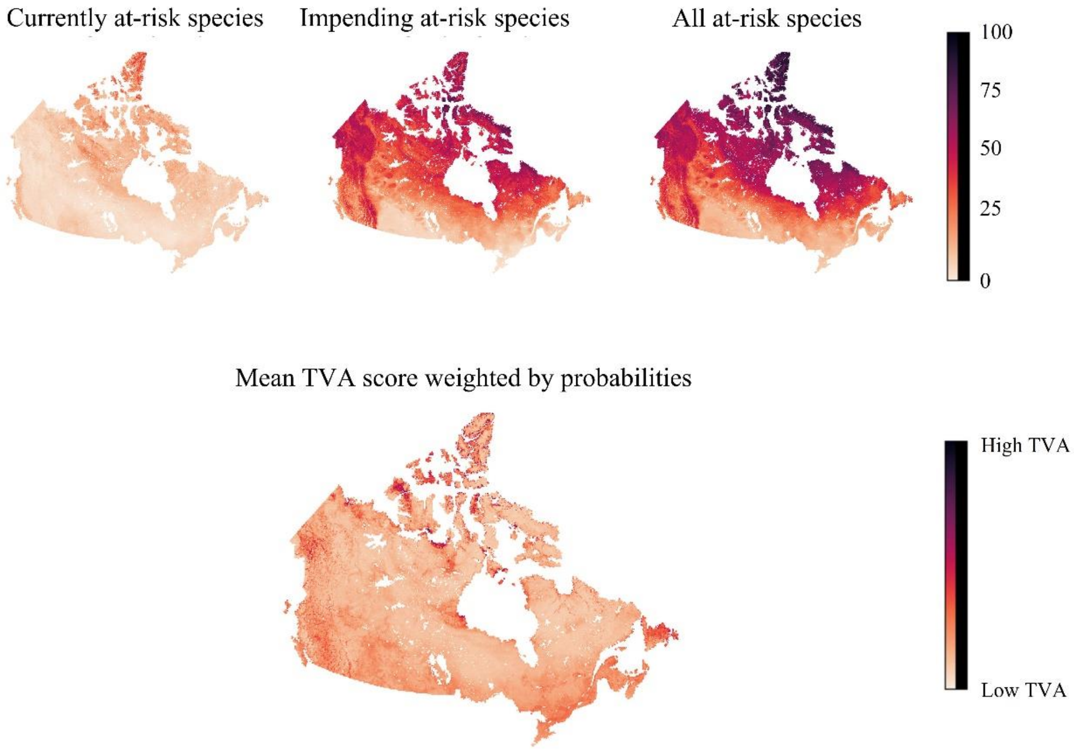

Figure 4. Top left: Percent of species present in each cell that are currently at-risk species (i.e. currently listed as near threatened, vulnerable, endangered or critically endangered). Top middle: Percent of species present in each cell that are impending at-risk species (i.e. species with a TVA score greater than currently vulnerable species). Top right: All at risk species (current and impending at-risk species combined). The bottom map displays the mean TVA score of each species present in a cell, weighted by their probability of being present.

Tables

Table 1. Top ten species which are currently listed as least concern and whose TVA score is greater than the average score of species currently listed as vulnerable (x̄ = 1.09). See supplementary material for the full list of 83 species highlighted.

Common Name	Scientific Name	Dietary Guild[1]	Breeding Biome[2]	Life History Guild[3]	TVA Score
Golden Eagle	*Aquila chrysaetos*	VertFishScav	Habitat Generalist	Birds of Prey	2.06
Pine Grosbeak	*Pinicola enucleator*	PlantSeed	Boreal Forest	Forest Birds	2.05
Northern Goshawk	*Accipiter gentilis*	VertFishScav	Forest Generalist	Birds of Prey	2.04
Surf Scoter	*Melanitta perspicillata*	Invertebrate	Wetland	Waterfowl	1.95
Short-eared Owl	*Asio flammeus*	VertFishScav	Habitat Generalist	Grassland Birds	1.93
Barrow's Goldeneye	*Bucephala islandica*	Invertebrate	Wetland	Waterfowl	1.93
Red-throated Loon	*Gavia stellata*	VertFishScav	Arctic Tundra	Wetland Birds	1.88
Northern Fulmar	*Fulmarus glacialis*	VertFishScav	Coasts	Seabirds	1.87
Canada Jay	*Perisoreus canadensis*	Omnivore	Boreal Forest	Forest Birds	1.87
American Three-toed Woodpecker	*Picoides dorsalis*	Invertebrate	Boreal Forest	Forest Birds	1.82

[1] Elton Traits 1.0: Species-level foraging attributes of the World's birds and mammals (Wilman *et al.* 2014)
[2] Decline of the North American avifauna (Rosenberg *et al.*, 2019)
[3] NABCI: State of Canada's Birds 2019 (NABCI 2019)

Table 2. Linear model results predicting change in species abundance with SDM predictions, TVA index, exposure, adaptive capacity, and sensitivity. Also see Fig. S2.

Metric	Estimate	Standard Error	P Value
SDM Predictions	0.69	0.24	0.0038
TVA Score	-0.26	0.12	0.033
Exposure	-1.31	0.23	3.69e-08
Adaptive Capacity	-0.55	0.26	0.038
Sensitivity	0.71	0.28	0.013

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Appendix

SDM specifications - We ran each species through three models: Generalized Additive Model (GAM), Boosted Regression Tree (BRT), and Maximum Entropy (MaxEnt) model. Here, We used the *mgcv* package in R (R Core Team, 2020) to run the GAMs with a binomial family and logit link function. BRTs is a machine learning technique that uses two algorithms: decision trees and boosting (Elith et al., 2008). BRTs iteratively splits the predictor data creating a simple model each time, which are combined to produce a final optimized model for predictions (Eskildsen et al., 2013). For this model, we used the *gbm* package in R, using a Bernoulli family, tree complexity of four, learning rate of 0.008 and bagging fraction of 0.5. The MaxEnt models also models non-linear relationships while maximizing the entropy of the raw distribution (Elith et al., 2010; Bateman et al., 2020). We ran the MaxEnt models using the *dismo* package in R using default settings.

TVA indexing - Traits included in the TVA (Table S1) were extracted from the curated trait's dataset. Traits reflecting sensitivity were extracted and a quantitative index was created for foraging strata. The foraging strata diversity index was set such that generalists were given a value of three, species utilizing two foraging stratums were given a value of two, and single foraging strata species were given a value of one, these values were then log scaled. Persistence was estimated by summing foraging strata, innovativeness, and generation length and subsequently downscaled between zero and one, such that values closer to one represented lower persistence ability (low foraging habitat diversity, low innovativeness, and long generation length). Sensitivity was estimated by summing the persistence value with the relative loss in suitable habitat for each species (Fig. 1A). Traits included in the adaptive capacity component were extracted and a quantitative index was created for the migration traits. The migration index was set between zero and three based on migration distance (non, migratory, long, or short) and migration status (non-migratory, obligate, or facultative). Long-distance, obligate migrants have better dispersal ability and given a value of three, whereas than non-migratory birds were given a value of zero. The migration index, in addition to clutch size, the number of habitats (log scaled of habitat diversity) and gain in suitable habitat, were downscaled between zero and one, such larger values represent better dispersal ability (higher migration index, larger clutch size, greater habitat diversity) and a larger gain in suitable habitat (Fig. 1B). To calculate dispersal ability, the migration index, habitat diversity, and clutch size were summed. The dispersal value and gain in suitable habitat were then summed to estimate overall adaptive capacity for each species. Exposure was estimated by summing the number of additional IUCN threats and net loss in suitable habitat. These two traits were normalized between zero and one, such that one represents higher exposure (many additional threats and large net loss in suitable habitat; Fig. 1C).

Change in species abundance - We obtained the estimated North American population size (popest; between 1970 – 2017) and the estimated loss of breeding individuals (loss_med) over the same period from Rosenberg et al., (2019)(Rosenberg et al., 2019), for all birds included in both datasets (n = 411). Change in abundance was estimated using the following formula:

$$Percent\ change\ in\ abundance = \frac{Population\ estimate\ \times (-1)}{Estimated\ loss\ of\ breeding\ individuals}$$

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Supplementary Figures and Tables

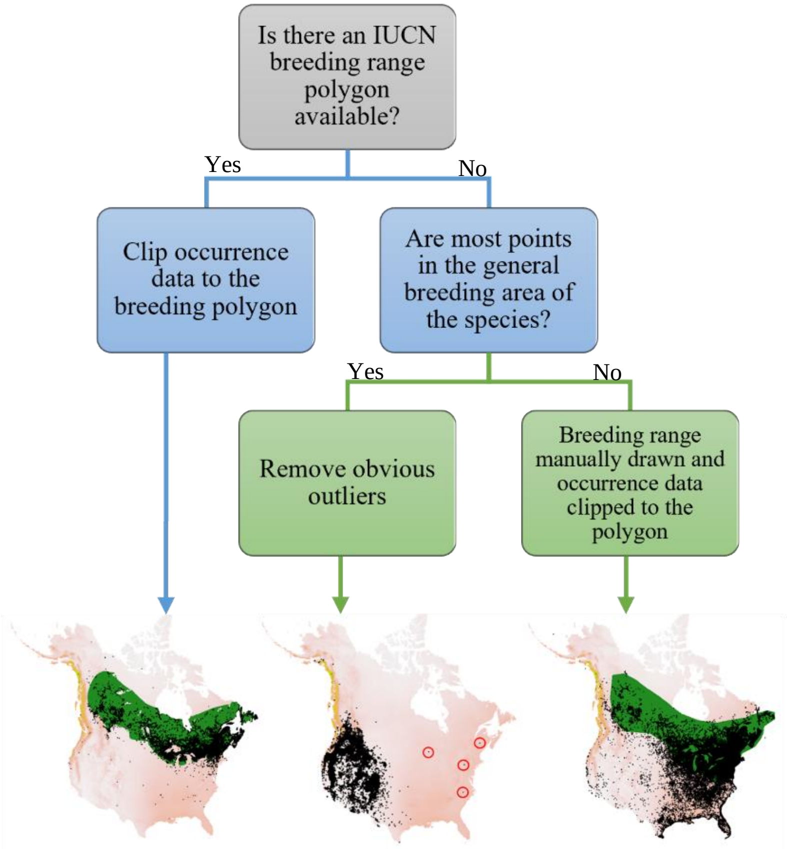

Figure S1. Occurrence data extraction from GBIF and data cleaning workflow for all 471 species of birds breeding in Canada. See *occurrence data* section in methods of main text for more details.

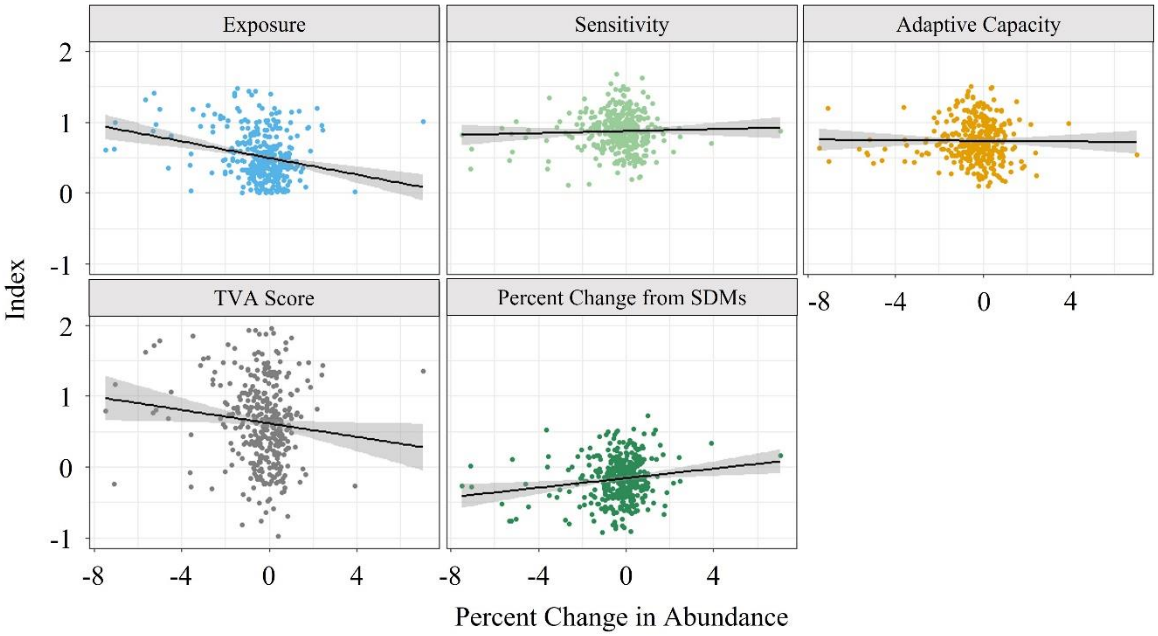

Figure S2. Relationship between change in abundance and percent change in suitable habitat from SDM, overall TVA score and each TVA components.

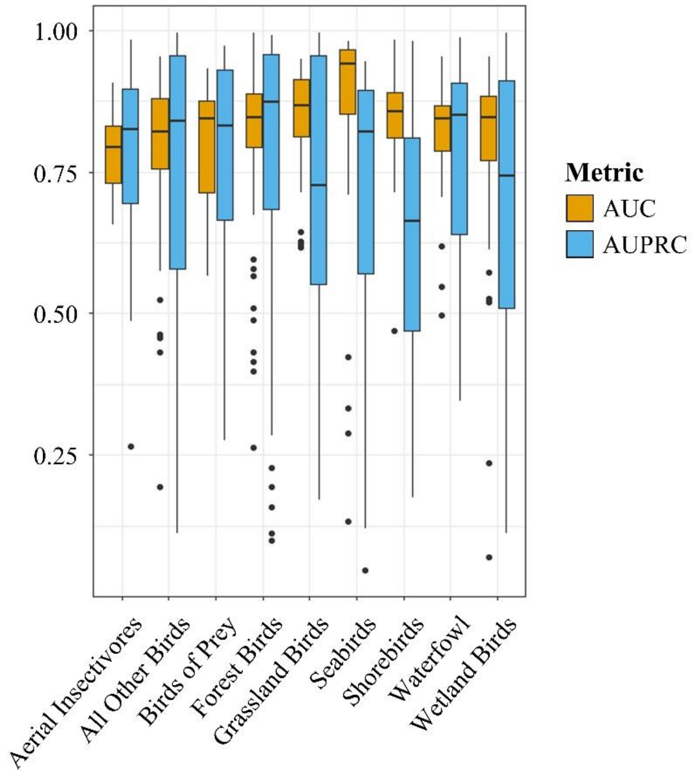

Figure S3. Species distribution model validation metrics (AUC and AUPRC) across Canada

Table S1. Variables and traits included in SDMs and TVA, respectively.

SDM Variables	Predictor Variables	
Climatic[1]	Mean Annual Precipitation (mm)	
	Degree-days below 0°C (Chilling degree days)	
	Precipitation as snow (mm)	
	Hargreave's climatic moisture index	
	Degree-days above 18°C	
Topographic	Topographic wetness index	
	Topographic ruggedness index	
	Land cover	
TVA Components	Traits	
Sensitivity	Persistence Ability	Number of Foraging Strata (Log scaled)
		Total Innovations
		Generation Length
	Loss in Suitable Habitat[2]	
Adaptive Capacity	Dispersal Ability	Number of Habitats (Log scaled)[3]
		Clutch Size
		Migration Index[4]
	Gain in Suitable Habitat[2]	
Exposure	Number of Threats[5]	
	Net Loss in Suitable Habitat[2]	

[1] *AdaptWest Project 2021*

[2] *SDM predictions*

[3] *Number of habitats listed by IUCN*

[4] *Index is a combination of migration distance (long or short) and status (obligatory or facultative)*

[5] *Number of threats listed by IUCN, excluding "Climate change and sever weather"*

Table S2. Species currently listed as least concern and were identified with having a TVA score greater than the average score of species currently listed as vulnerable ($\bar{x}$ = 1.09).

Common Name	Scientific Name	Dietary Guild[1]	Breeding Biome[2]	Life History Guild[3]	TVA Score
Golden Eagle	*Aquila chrysaetos*	VertFishScav	Habitat Generalist	Birds of Prey	2.20
Northern Fulmar	*Fulmarus glacialis*	VertFishScav	Coasts	Seabirds	2.00
King Eider	*Somateria spectabilis*	Invertebrate	Arctic Tundra	Waterfowl	1.89
Barrow's Goldeneye	*Bucephala islandica*	Invertebrate	Wetland	Waterfowl	1.86
Surf Scoter	*Melanitta perspicillata*	Invertebrate	Wetland	Waterfowl	1.74
Short-eared Owl	*Asio flammeus*	VertFishScav	Habitat Generalist	Grassland Birds	1.68
Parakeet Auklet	*Aethia psittacula*	Invertebrate	Coasts	Seabirds	1.68
Black Guillemot	*Cepphus grylle*	VertFishScav	Coasts	Seabirds	1.61
White-rumped Sandpiper	*Calidris fuscicollis*	Invertebrate	Arctic Tundra	Shorebirds	1.60
Dunlin	*Calidris alpina*	Invertebrate	Arctic Tundra	Shorebirds	1.59
Common Murre	*Uria aalge*	VertFishScav	Coasts	Seabirds	1.57
Tufted Puffin	*Fratercula cirrhata*	VertFishScav	Coasts	Seabirds	1.55
Townsend's Solitaire	*Myadestes townsendi*	Omnivore	Western Forest	Forest Birds	1.54
Ferruginous Hawk	*Buteo regalis*	VertFishScav	Grassland	Birds of Prey	1.51
Pigeon Guillemot	*Cepphus columba*	VertFishScav	Coasts	Seabirds	1.50
American Oystercatcher	*Haematopus palliatus*	Invertebrate	Coasts	Shorebirds	1.48
Willow Ptarmigan	*Lagopus lagopus*	PlantSeed	Arctic Tundra	All Other Birds	1.47
Thick-billed Murre	*Uria lomvia*	VertFishScav	Coasts	Seabirds	1.47
Red-throated Loon	*Gavia stellata*	VertFishScav	Arctic Tundra	Wetland Birds	1.39
American Pipit	*Anthus rubescens*	Invertebrate	Arctic Tundra	All Other Birds	1.39
Hudsonian Godwit	*Limosa haemastica*	Invertebrate	Wetland	Shorebirds	1.37
Horned Puffin	*Fratercula corniculata*	VertFishScav	Coasts	Seabirds	1.35

Gray-cheeked Thrush	*Catharus minimus*	Invertebrate	Boreal Forest	Forest Birds	1.33
Pelagic Cormorant	*Phalacrocorax pelagicus*	VertFishScav	Coasts	Seabirds	1.32
Williamson's Sapsucker	*Sphyrapicus thyroideus*	Omnivore	Western Forest	Forest Birds	1.31
Glaucous-winged Gull	*Larus glaucescens*	VertFishScav	Coasts	Seabirds	1.30
Baird's Sparrow	*Ammodramus bairdii*	Omnivore	Grassland	Grassland Birds	1.30
Black Turnstone	*Arenaria melanocephala*	Invertebrate	Coasts	Shorebirds	1.28
Smith's Longspur	*Calcarius pictus*	Omnivore	Arctic Tundra	All Other Birds	1.26
Purple Sandpiper	*Calidris maritima*	Invertebrate	Arctic Tundra	Shorebirds	1.26
Ross's Gull	*Rhodostethia rosea*	Invertebrate	Coasts	Seabirds	1.25
Northern Gannet	*Morus bassanus*	VertFishScav	Coasts	Seabirds	1.25
Bluethroat	*Luscinia svecica*	Invertebrate	Other	All Other Birds	1.22
Gray-crowned Rosy-Finch	*Leucosticte tephrocotis*	PlantSeed	Other	All Other Birds	1.20
Fox Sparrow	*Passerella iliaca*	Omnivore	Forest Generalist	Forest Birds	1.20
Ancient Murrelet	*Synthliboramphus antiquus*	Invertebrate	Coasts	Seabirds	1.19
Iceland Gull	*Larus glaucoides*	VertFishScav	Wetland	Wetland Birds	1.16
Stilt Sandpiper	*Calidris himantopus*	Invertebrate	Arctic Tundra	Shorebirds	1.14
White-crowned Sparrow	*Zonotrichia leucophrys*	PlantSeed	Habitat Generalist	All Other Birds	1.14
Sanderling	*Calidris alba*	Invertebrate	Arctic Tundra	Shorebirds	1.13
Common Ringed Plover	*Charadrius hiaticula*	Invertebrate	Coasts	Shorebirds	1.12
Prairie Falcon	*Falco mexicanus*	VertFishScav	Arid lands	Birds of Prey	1.09
Rock Sandpiper	*Calidris ptilocnemis*	Invertebrate	Arctic Tundra	Shorebirds	1.08
Brewer's Sparrow	*Spizella breweri*	Omnivore	Arid lands	All Other Birds	1.06
Dark-eyed Junco	*Junco hyemalis*	PlantSeed	Forest Generalist	Forest Birds	1.05
Lewis's Woodpecker	*Melanerpes lewis*	Invertebrate	Western Forest	Forest Birds	1.04
Northern Goshawk	*Accipiter gentilis*	VertFishScav	Forest Generalist	Birds of Prey	1.04

Northern Shrike	*Lanius borealis*	VertFishScav	Arctic Tundra	All Other Birds	1.03
Mountain Bluebird	*Sialia currucoides*	Invertebrate	Western Forest	All Other Birds	1.02
Ruddy Turnstone	*Arenaria interpres*	Invertebrate	Arctic Tundra	Shorebirds	1.01
Pacific Loon	*Gavia pacifica*	VertFishScav	Wetland	Wetland Birds	1.01
Pectoral Sandpiper	*Calidris melanotos*	Invertebrate	Arctic Tundra	Shorebirds	1.00
Western Sandpiper	*Calidris mauri*	Invertebrate	Arctic Tundra	Shorebirds	0.99
Eastern Yellow Wagtail	*Motacilla tschutschensis*	Invertebrate	Other	All Other Birds	0.98
Sage Thrasher	*Oreoscoptes montanus*	Invertebrate	Arid lands	All Other Birds	0.98
Henslow's Sparrow	*Ammodramus henslowii*	Invertebrate	Grassland	Grassland Birds	0.97
Greater Scaup	*Aythya marila*	Invertebrate	Arctic Tundra	Waterfowl	0.97
Trumpeter Swan	*Cygnus buccinator*	PlantSeed	Wetland	Waterfowl	0.97
Vesper Sparrow	*Pooecetes gramineus*	Omnivore	Grassland	Grassland Birds	0.96
Gyrfalcon	*Falco rusticolus*	VertFishScav	Arctic Tundra	Birds of Prey	0.95
Harlequin Duck	*Histrionicus histrionicus*	Invertebrate	Wetland	Waterfowl	0.94
Glossy Ibis	*Plegadis falcinellus*	Invertebrate	Wetland	Wetland Birds	0.94
Pacific Golden-Plover	*Pluvialis fulva*	Invertebrate	Arctic Tundra	Shorebirds	0.93
Red-headed Woodpecker	*Melanerpes erythrocephalus*	Invertebrate	Eastern Forest	Forest Birds	0.91

[1] Elton Traits 1.0: Species-level foraging attributes of the World's birds and mammals (Wilman *et al.* 2014)

[2] Decline of the North American avifauna (Rosenberg *et al.,* 2019)

[3] NABCI: State of Canada's Birds 2019 (NABCI 2019)

Linking statement: From biological traits to abundance data to improve SDMs

Integrating biological traits and species distribution models could improve overall climate change vulnerability assessments. Such assessments would be more thorough and accurate assessments since they are based on the geographic change in suitable habitat experienced by each species as well as their sensitivity, adaptive capacity, and exposure to climate change. However, including biological traits is not the only avenue available to improve model performance and predictions. Abundance data can provide more insightful relationships between species and their habitat. Given the recent and numerous methods developments made for SDMs combined with the sparsity of data in many locations, determining efficient and effective approaches to combining disparate datasets is critical. For my next chapter, I ask whether combining presence-absence data with survey data yields better predictions than either data type in isolation.

Comparing species distribution models using occurrence, abundance-weighted and abundance data

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Abstract

Context Species distribution models (SDM) are at the center of climate change assessments. While having been very useful in the past, many argue that the traditional presence-absence data used for these models is insufficient. Abundance data, or count data, could provide more insightful model outputs since they can quantify how many species are predicted to be present in an area of interest. Despite requiring more resources to obtain such data, abundance-based models tend to perform better then occurrence-based models. However, a recently developed weighting approach has been shown to improve model performance. Therefore, we investigate the best approach to utilize abundance data by comparing model performance from four different models: (1) abundance-based model, (2) occurrence-based model weighted by abundance, and (3-4) presence-absence data from two different sources. We compared the explanatory and predictive power of all four models using linear models and calculated eight performance metrics for the occurrence-based models, as well as two performance metrics for the abundance-based models. The Weighted model outperformed the other three models in explanatory power, while the Abundance model only outperformed the two other presence-absence models (3-4) in explanatory power. The explanatory power of the Weighted model was significantly related to species abundance, and the Abundance models with species range size. However, the discrimination metric from the Abundance models was found to increase with species abundance. Using abundance data can improve SDM’s predictive power. However, we found that models which indirectly model abundance, i.e. occurrence data weighted by abundance, outperform models which directly model abundance. Many researchers argue that abundance models are a more appropriate metric to use for accurate SDMs, however we argue that occurrence models weighted by abundance could improve model performance.

Key words: *abundance, boreal forest, presence-absence, species distribution models, waterfowl, weighted model*

Introduction

As we enter an epoch of severe global change, it is clear that biodiversity around the world will be affected by climate warming. Species distribution models (SDM) are the most commonly used tool for understanding the enormity of these impacts (Elith and Leathwick, 2009; Lawler et al., 2011). These models use associations between where and when a species is observed, i.e. occurrence data, to predict a species potential distribution across a spatial and temporal landscape (Barker et al., 2014; Senay et al., 2013). The model predictions are used to better anticipate future change in the environment and are particularly valuable for remote, poorly surveyed areas, and areas experiencing increased warming rates such as Canada (Bush and Lemmen, 2019).

The interest in species distribution models using occurrence data has continued to increase over the years despite these models having some shortcomings and limitations (Lobo et al., 2010). One such limitation is the lack of true absence, or confirmed absence data, for presence-only models. These models are a subset of occurrence-based SDMs which use environmental data associated with presence records for a species to model its potential distribution (Senay et al., 2013). True absence data provide environmental data where a species is not present, but it is difficult to obtain and is usually unavailable, which leads researchers having to use “pseudo-absences” (Senay et al., 2013, 2013). Pseudo-absences are “implied absence” and provide background data where a species has not been explicitly observed (Elith and Leathwick, 2009). However, there are many reasons why a species may be absent from a particular location, other then habitat unsuitability, which are not considered in SDMs. For example, species may appear absent due to sampling issues (e.g., site inaccessibility, present but undetected) or biological issues (e.g., species interactions (competition or predation) leading to local exclusion, local extinction, or absent due to migratory behavior; Barbet-Massin et al., 2012; Elith and Leathwick, 2009; Lobo et al., 2010; Senay et al., 2013). Further, there are different sampling methods for pseudo-absences which have been developed, each influencing model outputs differently but none of which have been shown to be a superior method (Iturbide et al., 2015). Despite the improved SDMs which have been developed and the different sampling methods available, pseudo-absences still remain as a major source of uncertainty with occurrence-based SDMs (Senay et al., 2013).

Using species distribution models with occurrence data, researchers can generate maps of habitat 'suitability' (Weber et al., 2017), but many argue that abundance-based models (models that use count data instead of occurrence data) are better metrics since they quantify the number of individuals within an area of interest (Johnston et al., 2015; Martínez-Minaya et al., 2018; Mi et al., 2017; Waldock et al., 2022). Modelling abundance trends can also act as a proxy for estimating environmental change in a particular location and can provide early warnings signs of population collapse (Waldock et al., 2022). In theory, spatial outputs from abundance models display areas of higher abundance, which imply better environmental suitability, and areas of lower abundance, which imply lower environmental suitability and increased extinction risk (Weber et al., 2017). Yet, there are many mixed findings on the abundance-habitat suitability relationship. For instance, a meta-analysis performed by Weber et al., (2017) found a general positive correlation between abundance and habitat suitability for various taxa, including vertebrates, invertebrates, and plants (Weber et al., 2017). In contrast, another study found little evidence of any abundance-suitability relationship across 246 mammal species and 158 tree species (Dallas and Hastings, 2018). Further research is needed on inferring environment change and habitat suitability from abundance models, however we also need to understand which models are more appropriate based on species ecology.

Given the lack of clarity in early studies investigating the similarities and differences in abundance versus occurrence data, we need to better understand when abundance data adds additional information beyond the more readily available occurrence data. There are many factors yet to be fully investigated including: data type (occurrence vs abundance, presence-only vs presence-absence), sampling protocols, spatial extent, biases associated with the data, and species life history. Therefore, this study aimed to assess model performance using both occurrence and abundance data for 18 waterfowl species in the Canadian western boreal forest. Using data from the Waterfowl Breeding Population and Habitat Survey (WBPHS), we assessed model performance between four different datasets: (1) abundance data from WBPHS, (2) occurrence data derived from WBPHS abundance data, (3) occurrence data weighted by abundance, and (4) occurrence data from the Global Biodiversity Information Facility (GBIF). Further, we aimed to determine how species attributes, i.e. species abundance and range size, may influence model performance and outputs.

Methods

Population Data - Waterfowl data was obtained from the WBPHS, which covers northern United States and Canada, including most of the Canadian western boreal forest (Fig. S1; Canada, 2015). We included data from 2000 to 2019 for 13 individual species and 5 species groups, referred to as species henceforth (Table 1; Silverman et al., 2022). From this, we derived three datasets; the first dataset, referred to as the Abundance dataset, consisted of abundance data where abundance was calculated as *total indicated pairs.* Total indicated pairs (TIP) estimates the number of pairs present based on raw observation, while considering life-history characteristic (Barker et al., 2014). For instance, TIP for 14 species (excluding SCAU spp., REDH, RUDU, and RNDU) was calculated as *TIP = 1*singles + 1*pairs*. For the remaining four species (SCAU spp., REDH, RUDU, and RNDU), TIP was calculated as *TIP = 1*pairs*, where singles refer to a one male or a small group of males without a visible female associated with them, and pairs refers to male-female pairs seen on a segment (Silverman et al., 2022). A value of zero was given to all species not observed within a particular segment during the data collection. The second datasets, referred to as the Occurrence dataset, included presence-absence data derived from the WBPHS abundance data, such that any value equal to or greater than one was assigned a one, representing a presence, and a zero given to all other species not observed within a segment, representing absences. The third dataset, referred to as the Weighted dataset, consisted of abundance-weighted occurrence data. Unlike presence-absence datasets, where all entries are equal, an abundance-weighted dataset could provide more information on habitat suitability such that a higher number of individuals at one site may reflect a great habitat suitability (Yu et al., 2020). Weights were calculated following Yu et al., (2020) methods and are based on individual species abundance and overall species richness in sites according to equations 1 and 2:

$$uw_{ij} = RA_{ij} \times Richness_i \qquad \text{Equation 1}$$

$$w_{ij} = \frac{uw_{ij} - \min(uw_{ij})}{\max(uw_{ij}) - \min(uw_{ij})} \times 100 + 1 \qquad \text{Equation 2}$$

Where *i* = site, *j* = species, *RA* = relative abundance, and *uw* = unscaled weight, and *w* is the scaled weight used to train the SDMs (Yu et al., 2020).

Lastly, we obtained occurrence data from the Global Biodiversity Informatics Facility (GBIF: gbif.org) as the fourth dataset, the GBIF dataset, to further investigate how unstructured, citizen science data influences model performance compared to WBPHS data, which used a more structed sampling protocol.

Environmental Data - Climatic predictor variables were obtained from Adapt West (AdaptWest Project, 2021). We included five climatic variables known to be significant in modelling species distribution for avian species at a 5-km^2 grid scale (Table 3; Bateman et al., 2020; Wilsey et al., 2019). Additionally, we included four topographic variables which included a ruggedness index, a wetness index, land cover and wetlands layer. The wetlands layer was obtained from the National Forest Information System (Hermosilla et al., 2018), where a cell was considered a wetland for at least 80% of the survey years (or 13 out of the 16 years). From this, we calculated the percent wetland for each grid cell.

Model description and comparison - For all four datasets, we performed separate species distribution models across all species. We used Generalized Additive Model (GAM) and a Boosted Regression Tree (BRT) using the *mgcv* and *dismo* packages in R (R Core Team, 2020), both models have been found to have high performance for species distribution models (Eskildsen et al., 2013). For the models predicting presence-absences (Occurrence, Weighted, and GBIF) eight model performance metrics were calculated (AUC, AUPRC, Kappa, Specificity-Sensitivity, No Omission, Prevalence, Equal Sensitivity and Specificity, and Sensitivity) using the *PRROC* and *dismo* packages in R. To determine which model had the highest predictive power, we identified which model produced the highest value for each performance metric across all species. To evaluate the performance of the abundance models, two diagnostic metrics were calculated: (1) discrimination, calculated as Spearman’s Rank Correlation, and (2) precision, calculated as the variance of predicted abundances divided by the variance of observed abundances (Norberg et al., 2019; Waldock et al., 2022). Finally, the distribution from all four datasets were mapped across the western boreal forest to explore how the spatial patterns differ between each dataset.

Model performance with range size and commonness – We performed a Linear Model (LM) followed by an ANOVA to compare the explanatory power (deviance explained) between all four models. To assess if there was a relationship between explanatory power and performance metrics with species total abundance and/or range size, we performed separate LMs for each metric, with the metric as the response and total observed abundance and range size as predictors. Range size was calculated by summing the number of cells a species was found present in, which was then multiplied by 25 km^2 (5 x 5 km resolution).

Results

Deviance explained - The Weighted models had the highest deviance explained ($\bar{x} = 0.76 \pm 0.20$; mean deviance explained ± s.d. here and after), followed by the Abundance models ($\bar{x} = 0.63 \pm 0.19$; Fig. 1), the Occurrence models ($\bar{x} = 0.45 \pm 0.16$; Fig. 1), and the GBIF model ($\bar{x} = 0.37 \pm 0.18$). Overall, the type of data used for each model influenced the model's deviance explained ($F_{3, 68} = 36.4$, $P < 0.01$) and all contrasts were significant except between the Occurrence and GBIF models ($P<0.01$; Fig. 2).

Model predictive performances – Overall, the Weighted models performed the best, having the greatest value for five or more metrics (including the highest *Equal Sensitivity and Specificity*, *Kappa*, and *Specificity-Sensitivity*) for 12 out of 18 species, and the top scores for four metrics for the remaining four species (Fig. 2). The Occurrence and GBIF models performed worse in most metrics for most species, with the notable exception being they performed better for AUC and AUPRC, metrics (especially AUC) that are commonly used to assess performance of occurrence-based SDMs. To evaluate the Abundance models, two metrics were calculated: (1) discrimination, and (2) precision. The mean discrimination was $\bar{x} = 0.72 \pm 0.12$, indicating high discrimination between low and high values of observed abundances, and the mean precision was $\bar{x} = 0.34 \pm 0.19$, indicating moderate model precision (Fig. 3).

Abundance and Range Size – There were mixed results for whether explanatory power (based on deviance explained) and predictive power (based on model performance metrics) were related to species abundance and range size (Table 2). Explanatory power increased with abundance for the Weighted model and Occurrence models but decreased with range size for the Abundance model and Occurrence models ($P<0.01$). Since the Weighted model had much greater explanatory power then the Occurrence and GBIF models, only the Weighted model performance metrics were used to evaluate the relationship between the diagnostic metrics with species abundance and range size. Several relationships between the Weighted model metrics and species abundance and range size were found (Table 2). Five metrics decreased with species abundance, while the remaining two metrics, AUC and AUPRC, increased with species abundance. Additionally, five Weighted model metrics decreased with range size, while AUC increased with range size. The discrimination metric from the Abundance models (Spearman's Rank correlation) increased with abundance ($P < 0.01$). No other significant relationships were found with the precision metrics (Table 2).

Spatial patterns from each model – Distribution maps from all four models in the western boreal forest displayed differing spatial patterns (Fig. 4). Abundance spatial outputs display increased predictions along the southern edge of the boreal forest, whereas the Weighted model displayed a more homogenous prediction of occurrences throughout the boreal forest. Interestingly, the Occurrence and GBIF models produced very contrasting spatial patterns. The GBIF model displays a high probability of occurrence along the southern edge of the western boreal, where as the Occurrence model displays much high probabilities of occurrence throughout the western boreal.

Discussion

Modelling the changes in suitable habitat for biodiversity is key to better understand how much environmental change species will experience. Changes in habitat and phenology, ecosystem structure, and range shifts are all important factors that will impact species survivorship as climate-driven change continues to increase in severity (IPCC, 2022). Abundance-based SDM in particular, can provide additional information on changes in population size and have the potential to infer habitat suitability based on abundance, but this requires further research (Nielsen et al., 2005; Weber et al., 2017). Here, we compared model performance between four different datasets (Fig. 1), to understand how different data types influenced model outputs. Overall, the Weighted model outperformed the three other models, having both better explanatory and predictive power. The explanatory power of the Weighted model and the discrimination metric of the Abundance model both increased with species abundance. Whereas the explanatory power of the Abundance model decreased with range size. Lastly, all four models displayed very different predicted spatial patterns.

Abundance vs occurrence models - Comparing model performance between occurrence (presence-pseudo absence data) and abundance data for species distribution models has been done for a variety of taxa (Howard et al., 2014; Waldock et al., 2022; Yu et al., 2020). Here, we found abundance-based SDMs produced a higher deviance explained compared to the occurrence-based models, consistent with findings from the literature. One study found that directly modelling abundance for both fish and bird species produced better models for 80% of the species included in their study (Waldock et al., 2022). The authors stated that modelling abundance directly can provide better quantification of changes in spatial abundance patterns (Waldock et al., 2022). While these results are encouraging for the use of abundance data with SDMs, we found that using abundance data indirectly with occurrence data may be a better approach. The Weighted dataset produced higher deviance explained than both occurrence datasets and the abundance data. Rather than directly modelling abundance, a weight is added to each presence and absence record which account for both local species abundance and species dominance. Therefore, species present at a site with high abundance relative to high overall specie richness are assigned a greater weight (Yu et al., 2020). The weighted technique used here was developed by Yu et al., (2020), who also found that the weighted models used in their study on fluvial fish outperformed traditional, un-weighted models. Similarly, Howard et al., (2014) incorporated abundance data in their species distribution models. Instead of using the abundance data to weight the occurrences, they compared models that were trained on abundance data with those trained on presence-absence data. The models trained on abundance data were converted to presence-absence predictions and were found to significantly improve model performance compared to the traditional presence-absence trained models (Howard et al., 2014). While Yu et al., (2020) and Howard et al., (2014) incorporate abundance data into their distribution models differently, both studies showed improved model performance when indirectly modelling abundance. Perhaps modelling abundance indirectly, using it to inform presence-absence data, is a better approach than directly modelling abundance, however this requires further research.

Deviance explained with abundance and range size – One of the goals of this research was to determine how species ecology, more specifically their abundance and range size, influenced model performance. These results suggest that, for Occurrence models, explanatory power is highest for abundant yet spatially restricted species. This could be explained by the more abundant species having more reliable presence data to better train the models. Moreover, smaller range size allows for a larger portion of the species range to be sampled, providing more thorough and complete dataset for the distribution models, although this can potentially artificially inflate metrics such as AUC. More widespread species with larger ranges sizes may not be appropriate for SDMs since they can have weaker associations with the environment across a large landscape (Waldock et al., 2022). This sampling issue was likely also influential for the Abundance models, which also improved for spatially-restricted species. Larger range sizes are difficult to sample completely, especially in the remote Canadian boreal forest.

Model metrics with species abundance and range size - There were multiple relationships found between these variables, each varying in direction and significance (Table 2). Each model metric implies something different about the structure of the data, however seeing that the Weighted model is a new approach, using multiple diagnostic metrics can limit biases and inaccurate interpretation of the results (Yu et al., 2020). Of the two Abundance model metrics, discrimination was the only one to have any significant relationship with species abundance, such that larger species abundance increases the discrimination value (Table 2). Discrimination reflects how well a model discerns between low and high values of observed abundance (Norberg et al., 2019; Waldock et al., 2022). Identifying and tracking changes in abundance across a spatial and temporal scale is often needed for conservation and wildlife management, making this diagnostic metric particularly valuable (Waldock et al., 2022). Increased abundances would most likely increase the contrast between areas with low and high abundances, leading to better predictive power by the models.

Spatial patterns from each model – Although we cannot directly compare the spatial outputs from the Abundance models with the outputs from the three other models, we can still observe relative differences in the spatial distribution displayed (Fig. 5). Abundance and occurrence data have often produced dissimilar spatial patterns in previous work, most likely due to the influence of different biological processes between abundance and occurrence (Johnston et al., 2015; Mi et al., 2017; Nielsen et al., 2005).

The differing spatial outputs between the Abundance model and the three other models further support the findingsthat modelling and predicting species distributions using only occurrence or abundance data may be insufficient and lead to very contrasting conclusions. Interestingly, the models using occurrence data from two different sources (Occurrence and GBIF models) produced differing spatial distributions (Fig. 5). The GBIF map displays a high probability of occurrence at the southern edge of the western boreal, most likely due to the high spatial bias associated with unstructured citizen science data. Contrastingly, the occurrence data derived from WPBHS produced a much more heterogenous spatial pattern across the western boreal, further supporting the efficacy of a structured sampling protocol which could be used to collect both occurrence and abundance data.

Conclusion - While promising new more complex approaches are being developed for combining survey and presence-only data (e.g. Howard et al., 2014; Adde et al., 2021), these approaches are more computationally intensive and have so far been limited to a handful of species. Adde et al., (2021) applied an integrated species distribution modelling (ISDM) framework recently formalized by Isaac et al., (2020) on three waterfowl species in the western boreal forest. This approach integrated standardized survey data from WBPHS and unstructured citizen science data from eBird (Sullivan et al., 2009) to model species distributions where WBPHS data was limited (Adde et al., 2021). Although this more sophisticated approach has much potential to improve model performance, it may be impractical for studies with multiple species or for more cryptic and rare species.

Our results suggested that indirectly modelling abundance by using a weighted approach produced improved model performance. Moreover, based on the differing predicted spatial patterns from all four models, only using occurrence or abundance data is insufficient for conservation purposes. These findings support the use of the abundance-weighted approach when abundance data is available. Using approaches which indirectly model abundance can provide more informed interpretations about spatial prioritization, species spatial distribution as well as spatial and temporal changes in species abundance, all of which are vital for accurate conservation and wildlife management.

Figures

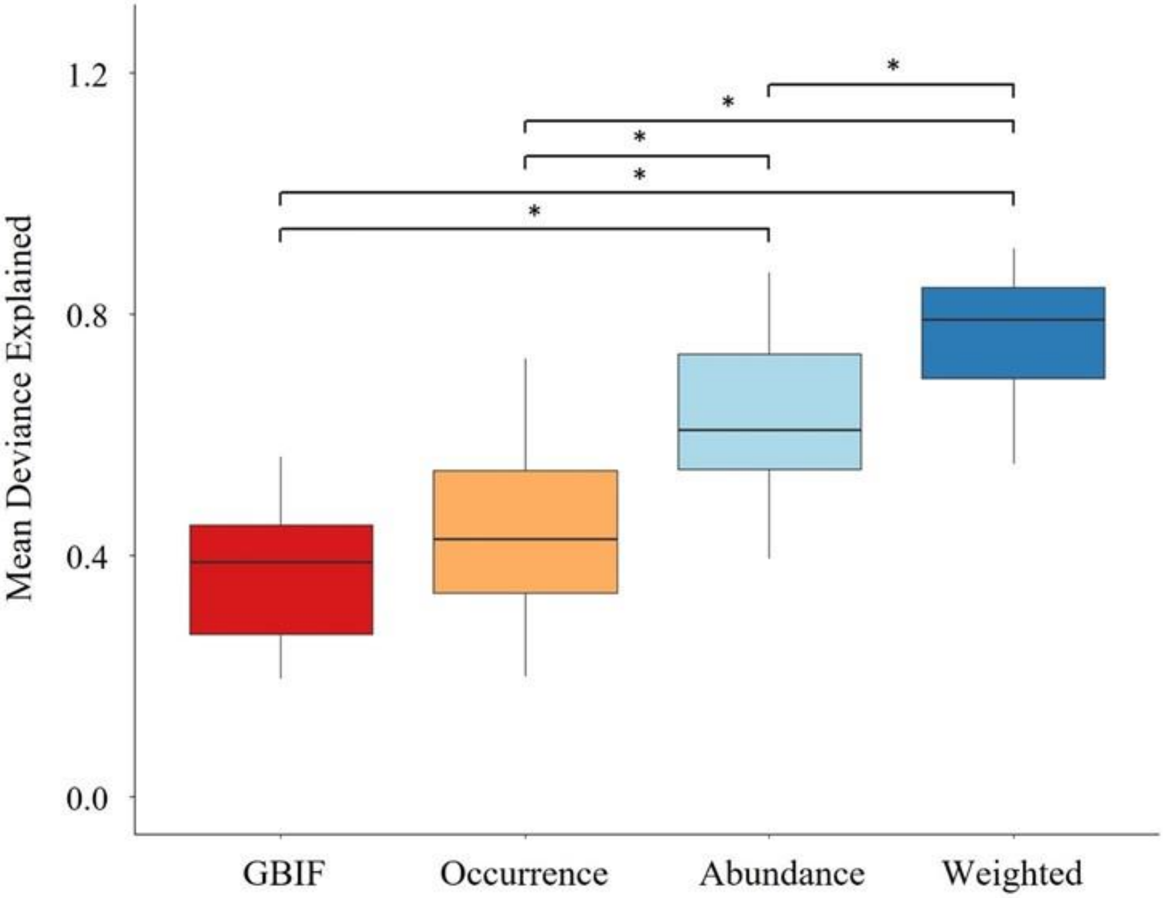

Figure 1. Deviance explained by for all four models; the bolded line in the boxes displays the mean deviance explained, with the whisker displaying the maximum and minimum distribution of the data. All contrasts were significant except between the Occurrence and GBIF models (P<0.01), where alpha = 0.05.

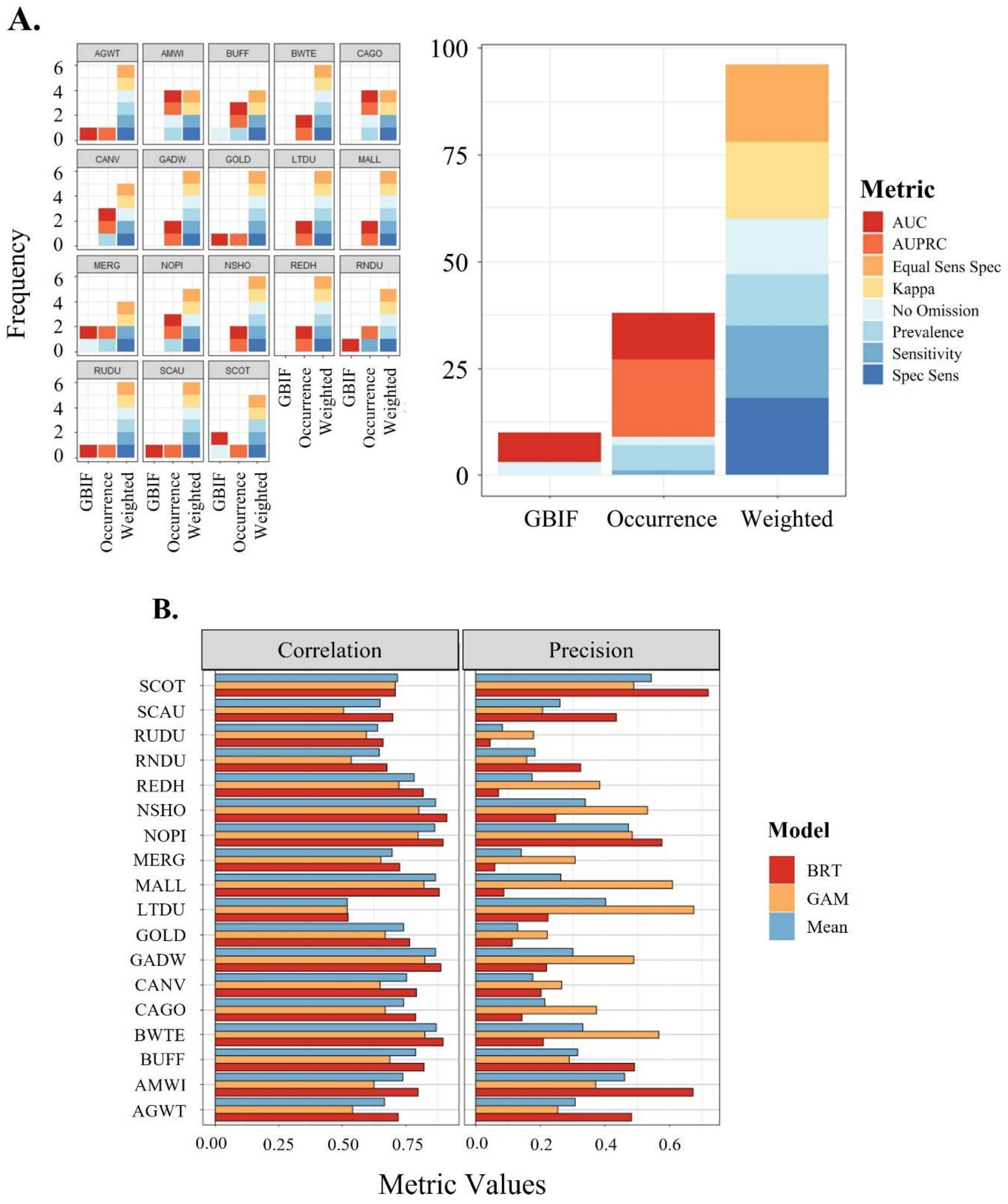

Figure 2. Diagnostic metrics calculated to the assess predictive power all four models across all 18 waterfowl species. **A.** Eight model performance metrics were calculated for the Weighted, Occurrence, and GBIF. The left panel displays which model produced the highest metric value for each species. The right panel displays which model produced the highest metrics across all species. **B.** The two Abundance model metrics performance across all species.

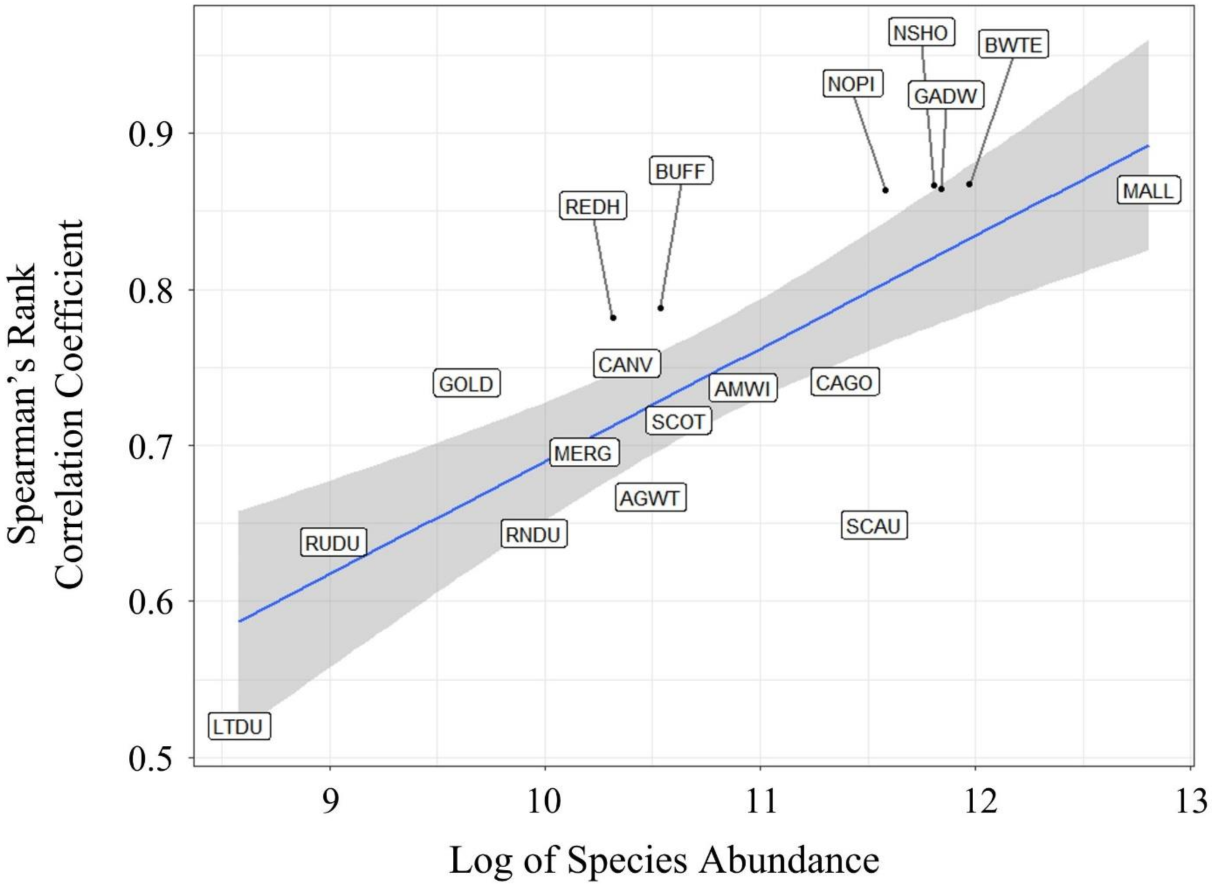

Figure 3. A significant positive relationship between the discrimination metric of the Abundance models and total species abundance, such that the discrimination correlation coefficient increases with increased species abundance. The species abundance is displayed on a logarithmic scale. The discrimination metric is calculated as Spearman's Rank Correlation coefficient. Labels represent species, see Table 1 for full common and scientific names.

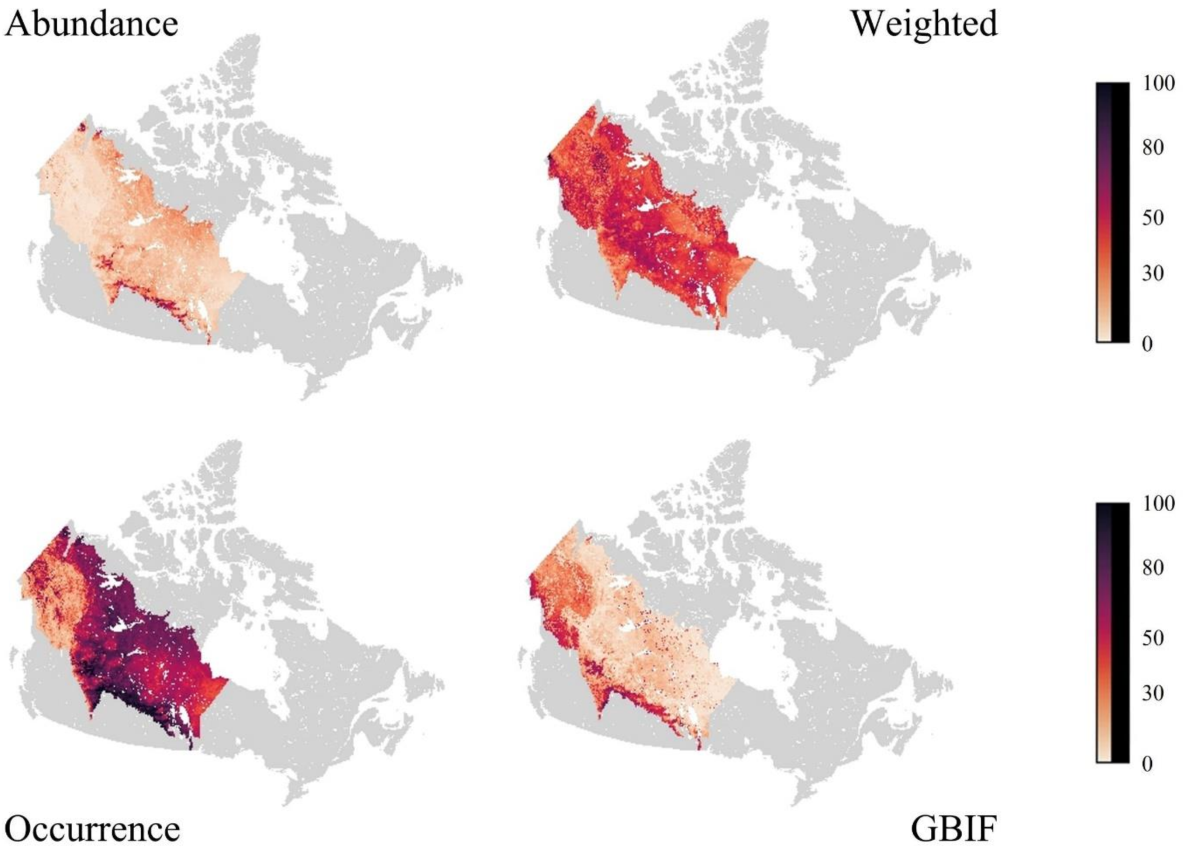

Figure 4. The predicted spatial distributions from all four models across the Canadian western boreal forest. Model predictions were summed across species and rescaled between zero and 100 for easier comparison. The Abundance map (top left) displays the predicted abundance of all 18 waterfowl species included in this study in the western boreal forest (scaled). The Weighted, Occurrence and GBIF maps (top right and bottom) display the predicted probability of occurrence for the 18 waterfowl species included in this study in the western boreal forest.

Tables

Table 1. Species and species groups included in this study. Species grouped according to Western Breeding and Population Habitat Survey.

Species Code	**Common Name**	**Scientific Name**
AGWT	Green-winged Teal	*Anas crecca*
AMWI	American Wigeon	*Mareca americana*
BUFF	Bufflehead	*Bucephala albeola*
BWTE	Blue-winged Teal	*Spatula discors*
CAGO	Canada Goose	*Branta canadensis*
CANV	Canvasback	*Aythya valisineria*
GADW	Gadwall	*Mareca strepera*
GOLD	Barrow's Goldeneye Common Goldeneye Long-tailed Duck	*Bucephala islandica* *Bucephala clangula* *Clangula hyemalis*
MALL	Mallard	*Anas platyrhynchos*
MERG	Hooded Merganser Common Merganser Red-breasted Merganser	*Lophodytes cucullatus* *Mergus merganser* *Mergus serrator*
NOPI	Northern Pintail	*Anas acuta*
NSHO	Northern Shoveler	*Spatula clypeata*
REDH	Redhead	*Aythya americana*
RNDU	Ring-necked Duck	*Aythya collaris*
RUDU	Ruddy Duck	*Oxyura jamaicensis*
SCAU	Greater Scaup Lesser Scaup	*Aythya marila* *Aythya affinis*
SCOT	Surf Scoter White-winged Scoter Black Scoter	*Melanitta perspicillata* *Melanitta deglandi* *Melanitta nigra*

Table 2. Results from LMs between deviance explained and diagnostic metrics with species abundance and range size.

Response Variable	**Significance (Estimate; P-value)**		
	Abundance	Range Size	Abundance: Range Size
Deviance Explained			
Abundance	-	-5.28e-06; P = 0.0062	-
Weighted	2.51e-06; P = 0.032	-	-
Occurrence	2.75e-06; P = 0.0043	-5.83e-06; P = 0.00028	-3.18e-11; P = 0.023
GBIF	-	-	-
Weighted Model Metrics			
Specificity-Sensitivity	-2.47e-05; P = 0.0065	-2.61e-05; P = 0.041	1.12e-09; P = 1.08e-07
Prevalence	-1.37e-05; P = 0.0039	-	4.64e-10; P = 2.5e-06
Equal Sensitivity Specificity	-5.28e-05; P = 3.33e-06	-	1.57e-09; P = 9.58e-10
Kappa	-3.38e-05; P = 0.0013	-4.35e-05; P = 0.0039	1.15e-09; P = 4.28e-07
Sensitivity	-2.30e-05; P = 0.00015	-1.46e-05; P = 0.048	8.14e-10; P = 1.22e-08
No Omission	-	-2.35e-05; P = 0.026	4.65e-10; P = 0.0003
AUC	1.84e-06; P = 0.0014	-4.21e-06; P = 2.96e-05	-1.99e-11; P = 0.015
AUPRC	1.83e-06; P = 0.00095	3.21e-06; P = 0.00025	-2.36e-11; P = 0.0037
Abundance Model Metrics			
Spearman's Rank Correlation	2.96e-06; *P* = 0.00096	-	-3.54e-11; P = 0.0061
Precision	-	-	-

Table 3. Predictor variables included in SDMs.

SDM Variables	Predictor Variables
Climatic[1]	Mean Annual Precipitation (mm) Degree-days below 0°C (Chilling degree days) Precipitation as snow (mm) Hargreave’s climatic moisture index Degree-days above 18°C
Topographic	Topographic wetness index Topographic ruggedness index Land cover Percent wetland[2]

[1] *AdaptWest Project 2021*

[2] *Hermosilla et al., 2018*

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Supplementary Figures

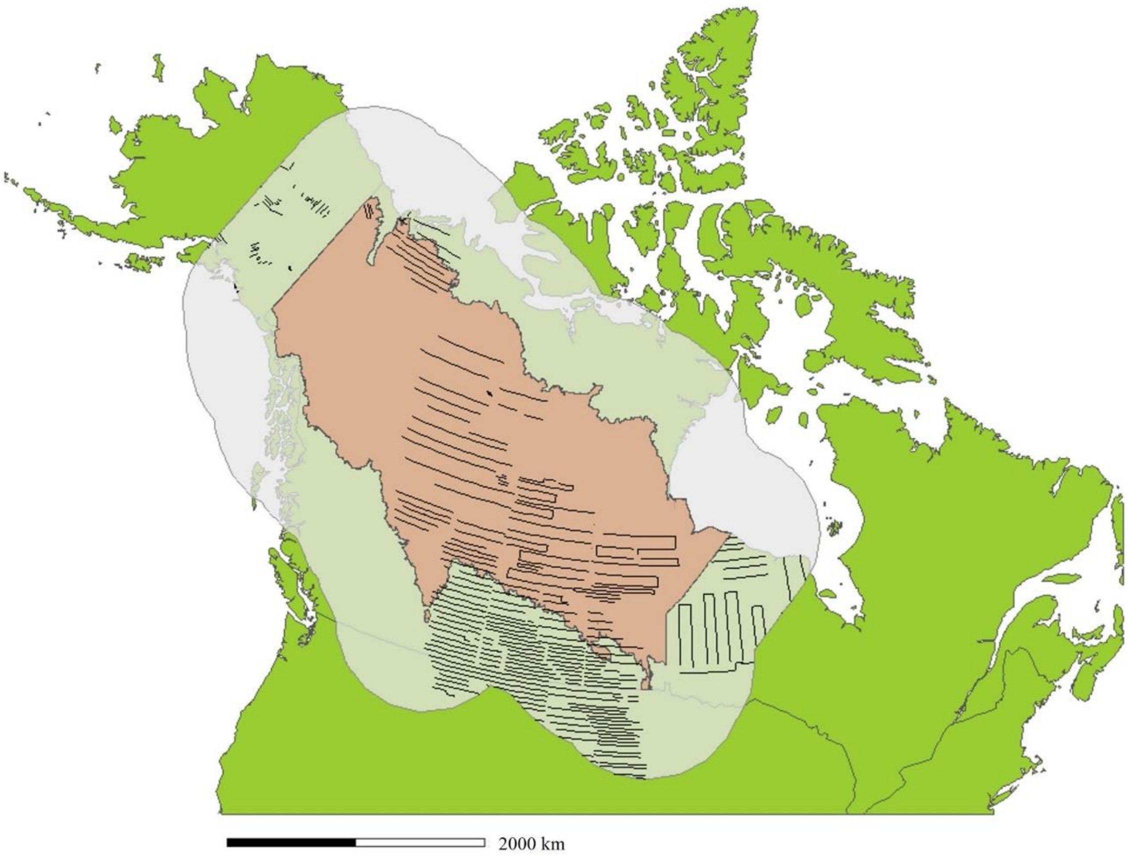

Figure S1. Map of the Western Boreal Forest, displayed by the red polygons, and the Waterfowl Breeding Population and Habitat Survey (WBPHS) aerial survey transects are displayed by the black lines. The species distribution models were trained on population and environmental data within the light grey polygon, which represents a 500 km buffer around the western boreal forest, to avoid truncating environmental variables.

Final Discussion

One major advantage of species distribution models is the ability to predict potential future distribution across a continuous landscape. These predictions are an essential tool for climate change research, spatial prioritization and wildlife and conservation management (Mi et al., 2017). SDMs are particularly valuable for areas that are undergoing rapid climate-driven change such as Northern Canada. Climate-driven change in Canada is responsible for many ecological changes being observed across the country, with changes in the Canadian Arctic even more drastic (IPCC, 2022). Given this, there is an urgent need to develop more accurate assessments of how climate-driven change will impact ecosystem structure, and species distribution and abundance. Despite the potential use for SDMs in such a fast-changing environment, these models contain many conceptual, biotic, and algorithmic shortcomings that are often left unaddressed and are a source of uncertainty (Elith et al., 2006; Howard et al., 2014). As the interest and use of SDM continues to increase, much research has been focused on improving the predictive performance of SDMs. Incorporating biological traits, abundance data, biotic interactions, and account for biases are only some of the avenues currently being explored to improve model predictions (Howard et al., 2014). Therefore, the overall goal of this thesis was to explore two such avenues that could improve species distribution models (Table 1).

First, I developed a trait vulnerability assessment (TVA) framework which incorporates SDM predictions more explicitly into each TVA component (sensitivity, adaptive capacity, and exposure). SDMs are used to predict environmental change and changes in habitat suitability for a species of interest. However, these models do not explicitly assess a species vulnerability to climate changes, but rather predict how much suitable habitat they are expected to lose with climate-driven change (Willis et al., 2015). Using SDMs, researchers can also predict how much suitable habitat a species is expected to gain as well as where these future suitable habitats will be located. However, these models do not consider a species ability to cope and adapt to such changes. For example, a case study on the Grey-necked Picathartes (*Picathartes oreas*) showed that SDMs predicted potential range expansion for this species. Yet the Grey-necked Picathartes was found to have low adaptive capacities due to its specialized nesting requirements which were not met in the potentially gained habitat (Willis et al., 2015). By integrating both SDMs and TVAs, a more complete and thorough assessment of each species vulnerability can be made. Such assessments would include information on how much habitat each species is predicted to gain or lose, as well as their ability to persist or disperse, given these environmental changes. Using the TVA framework developed in Chapter 1, I highlighted vulnerable avian guilds and provide key intel on which aspects of their life history are the main driver of their vulnerability (Table 1). With this information, more accurate and effected conservation and wildlife management practices can be implemented for endangered species and habitats.

For the second part of my thesis, I explored how different types of data influence model explanatory and predictive power. Abundance data has been nominated by many as a better metric for climate change modelling, simply because they provide a more quantitative continuous map of predictions. Rather than a binary, present or absent map, abundance-based model can produce predictions on the number of species expected to be in an area of interest (Howard et al., 2014; Mi et al., 2017; Martínez-Minaya et al., 2018; Yu et al., 2020). Some studies have compared models results between occurrence and abundance data (Howard et al., 2014; Johnston et al., 2015) while others have explored combining both occurrence and abundance data (Adde et al., 2021; Mi et al., 2017; Yu et al., 2020). Here, I compared model performance between both forms of data while also comparing a combined approach which uses abundance information to influence the occurrence data. My analysis determined that the combined approach produced models with higher explanatory and predictive power (Table 1). These results provide more support for the use of abundance data with SDMs; however, they also highlight the potential of using a combined approach rather than directly modelling abundance. Improving species distribution models is crucial to provide more accurate predictions, especially for areas such as Canada, where many drastic changes are already underway.

By including more species-specific information in species distribution models, such as biological traits and abundance data, researchers can produce more accurate and reliable model predictions needed for conservation and wildlife management. Including biological traits, as in trait vulnerability assessment, provides intel on the ability to cope and adapt with climate-driven change. A species sensitivity, adaptive capacity, and exposure to climate change greatly influences how severely they will experience changes in suitable habitat, which can help determine if and when these species need active conservation management (Willis et al., 2015). While including abundance data provides intel on the spatial distribution of relative abundances in an area of interest, it also can provide early warning signs of population decline and can potentially be used to infer habitat quality, although the latter requires more research (Howard et al., 2014). Further research could also explore different methodologies on combining occurrence and abundance data or integrating abundance-based SDMs with biological traits. By improving the predictive power of SDMs, researchers, conservation, and wildlife management as well as policy makers can better anticipate, and ideally, reduce climate-driven change impacts on biodiversity.

Tables

Table 1. Brief summary of chapter 1 and 2 included in this thesis.

Chapter	Aim	Methods	Main Findings
1. Integrating species distribution models with trait vulnerability assessment for Canadian birds	Develop a framework which includes more explicitly SDM predictions in all three TVA components.	Ran BRT, GAM, and MaxEnt distribution models. SDM predictions used as a trait in the TVA to reflect their sensitivity, adaptive capacity, and exposure to climate change. Evaluated the vulnerability of 471 birds breeding in Canada using this TVA.	Overall, seabirds are most vulnerable to climate change. Identified 83 species most likely to become vulnerable climate-driven changes due to their inability to disperse or persist or both. Identified three main breeding biomes used by more than 50% of vulnerable species: Artic Tundra, Wetlands, and Coastal habitats.
2. Comparing species distribution models using occurrence, abundance-weighted and abundance data	Explored best approach to use when working with abundance data. Further explored how species abundance and range size influence SDM outputs	Compared the predictive and explanatory power of SDM using four different datasets: (1) abundance data, (2) occurrence data weighted by abundance, (3-4) occurrence data from two different sources. Models were compared using various performance metrics for 18 waterfowl species in the Wester Boreal Forest.	The Weighted model significantly outperformed the other three models. The explanatory power of this model is positively related to species abundance. The Abundance models underperformed compared to the Weighted model but outperformed the two occurrence models. The explanatory power of the abundance models is negatively related to species range. The correlation coefficient between observed and predicted abundances from this model was positively related to species abundance.

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