Predicting the impact of climate change-induced resource loss on the endangered Golden-cheeked Warbler (*Setophaga chrysoparia*)

Leticia Santillana Fernández

A thesis
submitted in partial fulfillment of the
requirements for the degree of

Master of Science

University of Washington
2025

Committee:
Josh J. Lawler
Brian J. Harvey
Julie A. Heinrichs

Program Authorized to Offer Degree:
School of Environmental and Forest Sciences

University of Washington

Abstract

Predicting the impact of climate change-induced resource loss on the endangered Golden-cheeked Warbler (*Setophaga chrysoparia*)

Leticia Santillana Fernández

Chair of the Supervisory Committee:
Josh J. Lawler
School of Environmental and Forest Sciences

Although human land use has been the leading driver of endangerment, climate change continues to compound global biodiversity loss and poses a major risk to threatened and endangered species (Thomas et al. 2004, Chapin et al. Wilkening et al. 2019). For habitat specialists, such as the Golden-cheeked Warbler (*Setophaga chrysoparia*), climate change will have lasting consequences on habitat configuration, resource availability, phenology, and population densities (Wilkening et al. 2019, Maxwell et al. 2019). The Golden-cheeked Warbler, an endangered migratory songbird, breeds exclusively in the Ashe juniper (*Juniperus ashei*)-oak (*Quercus sp.*) woodlands of central Texas and depends on the shedding bark of mature juniper for nesting (Kroll 1980, Ladd and Gass 1999, Pulich 1976). Understanding how climate change will alter Golden-cheeked Warbler habitat is essential to the conservation of this at-risk species.

In this study, I explore how modeling approaches can be used to project the potential impacts of climate change on at-risk species, with the focus of informing landscape-level management decisions for the conservation of both the Golden-cheeked Warbler and Ashe juniper. In Chapter 1, I describe how I developed an ensembled species distribution model for Ashe juniper using edaphic, topographic and climatic predictor variables. I then used the best-performing model to project the potential future distributions of juniper through 2100 using the outputs from two

generalized circulation models (GCMs) run for two shared socio-economic pathways (SSPs). Across all models, I observed a contraction of the distribution of juniper within Texas. The juniper projections were then overlayed with a model of warbler densities to determine the potential loss of optimal and marginal warbler habitat through 2100 due to resource loss (Mueller et al. 2022). Under the most extreme climate scenario, the models predicted an almost complete loss of optimal and marginal warbler habitat, nearly 1,027 km^2 and 9,485 km^2, respectively. This approach detected areas where warbler habitat would persist even in the most extreme scenarios of climate-driven resource loss, allowing us to inform managers of areas of highest conservation priority.

In Chapter 2, with the support of my collaborators, I built a population model to simulate the effects of climate change-driven resource loss on the population responses of Golden-cheeked Warblers within Texas. Using the modeling platform HexSim, we leveraged literature and expert knowledge on the life history of the endangered warbler to parameterize a spatially explicit, individual-based model. I created a time series of habitat maps based on the work from Chapter 1. I then simulated warbler responses to a changing habitat under the same four climate scenarios. The model outcomes allowed me to determine the importance of selected protected areas to the persistence of warbler populations and confirm which of the areas could strategically be prioritized in conservation management. Results indicate that climate-induced resource loss has the potential to reduce warbler abundance by up to 94% in the most extreme climate scenarios (UKESM1-0-LL), with 10% and 51% reduction in the MPI-ESM1-2-HR SSP2-4.5 and SSP3-7.0 scenarios, respectively. At 4 out of 14 protected sites, our simulation forecasted complete loss of occupancy with the MPI-ESM1-2-HR SSP3-7.0 scenario but forecasted complete loss at 11 out of the 14 sites with the UKESM1-0-LL SSP2-4.5 scenario. Through this analysis, our model identified the Balcones Canyonlands Preserve, Balcones Canyonlands National Wildlife Refuge, and Fort Cavazos as containing important climate refugia. Our study presents the immense impact climate change will potentially have on the persistence of the endangered Golden-cheeked Warbler and its habitat. This work contributes to the scientific understanding of how complex modeling can be leveraged to inform landscape-level conservation efforts of at-risk species threatened by climate change.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

ACKNOWLEDGEMENTS

I first would like to thank Josh Lawler for all of his support and guidance over the past 2.5 years. It was a privilege to be a member of his lab and to engage with such a wide range of approaches to conservation. His mentorship and compassion have greatly contributed to my growth as a scientist and as a person. This work would not have been possible without the funding support from the Strategic Environmental Research and Development Program (SERDP) (grant no. RC22-3437) from the Department of Defense. I also want to thank the Bridging the Gap Fellowship and SEFS for all the funding support.

I want to acknowledge my committee member, Julie Heinrichs, for her endless support and patience in my journey of learning about population modeling. It was a pleasure to connect and collaborate with the entire Computational Ecology Group team. I am especially thankful for Sydney Watkins for the immense amount of wisdom—HexSim and beyond—she so patiently shared with me. I cannot imagine how this research would have turned out without all of Sydney's guidance and modeling expertise. I am also incredibly lucky to have received a tremendous amount of knowledge and assistance from Nathan Schumaker, who traveled to Seattle twice to bestow us with all the HexSim tips and tricks. I would also like to express my gratitude to my committee member, Brian Harvey, for all of the forest wisdom and guidance in navigating graduate school. I love that I now experience forests in such a beautiful way—thank you for all the enthusiasm and passion you have inspired in me.

I am incredibly grateful for everyone in the Landscape Ecology and Conservation Lab. Thank you, especially, to Fern Crossway and Leo Wahl for your never-ending support. From answering all my modeling questions to encouraging me to climb more, I am incredibly thankful to have shared my time in graduate school with you both.

I want to thank my Doris Duke Conservation Scholars Program community for all the unconditional support and guidance, and for all the years of building memories and dreams together. I also want to thank Bonnie Baird at the Woodland Park Zoo for being an incredible mentor and for reconnecting me with my love for animals. Huge shout out to Olive and her mob of Wallabies, Carson the Red Panda, and the Snow Leopards for constantly bringing me joy.

Lastly but most importantly, I want to thank my friends and family for the endless support I received as I completed my thesis and navigated some incredibly challenging years. No tengo palabras para expresar mi gratitud por el apoyo constante de mi familia. Muchas gracias a mi mamá y a mi papá por siempre creer en mí, y por darme energía y fuerza para seguir mis sueños. A Karla y a Ale, muchas gracias por seguir ahí cuando más los necesitaba y por la felicidad que siempre traen a mi vida. Muchas gracias a todas mis amigas y amigos por su apoyo, amistad y compañía. I am so lucky to be constantly inspired by all of you. To finish, huge thank you to my two adorable and incredibly goofy cats, Oso and Kuma, for always showing me unconditional love and nudging me to go to bed when I worked late.

INTRODUCTION

Anthropogenic climate change poses major threats to global biodiversity (Thomas et al. 2004; Chapin et al. 2000). Climate change is expected to continue to drive habitat loss and shifts in distributions resulting in negative effects on populations and species. Coupled with decreased landscape connectivity due to urbanization, climate change will further reduce the possibilities for species to adapt or disperse to suitable climatic conditions (Littlefield et al. 2019). A study focused on understanding the processes that lead to extinction found that an increase in maximum annual temperatures has been the most important factor in modern day extinctions and that a majority of the 538 species in that study would likely go extinct before successfully dispersing to new suitable conditions based on their past dispersal rates (Roman-Palacios & Wiens 2020). Without actions to mitigate climate change, Urban (2015) predicts that an increase in global temperature of 4.3˚C will threaten the persistence of 16% of species globally. With a 3˚C increase, 8.5% of species would be at risk, which emphasizes the importance of climate-change mitigation.

Shifts in climate patterns and disturbance regimes will likely affect vegetation regeneration, ecosystem function, and phenology, which can result in disruptions of interspecific interactions and limit species persistence (Harvey & Enright 2022; Twinning et al. 2022). All of these factors have already led some bird species to adapt by shifting their distributions and in some cases, have led to range contractions (Hitch & Leberg 2007, Bateman et al. 2020). With a 3.0˚C increase in global mean temperature by end of century, about two-thirds of birds in North America may be moderately to highly vulnerable to climate change (Bateman et al. 2020). For example, a key effect of climatic changes is the fundamental disruption of trophic interactions through changes in abundance and life history traits of consumer and resource species (Portalier et al. 2022, Twinning et al. 2022). Climate-driven changes in phenology can also have adverse impacts on species. Phenological mismatches are likely to be especially harmful for habitat specialists and migratory animals who cannot foresee resource and habitat conditions at breeding or foraging sites (Twinning et al. 2022, Both et al. 2009). With increases in the severity and frequency of extreme heat, the vegetation that birds depend on for habitat may become susceptible to drought-related stress and mortality, which can also intensify wildfire risk (Harvey & Enright 2022). Because at-risk species, such as the Golden-cheeked Warbler (*Setophaga chrysoparia*) are often habitat specialists and have reduced populations, climate change may disproportionately affect these species' adaptive capacity (Wilkening et al. 2019).

The Golden-cheeked Warbler is an endangered songbird that overwinters in Central America and migrates north to spend the breeding season entirely in Texas (Ladd and Gass 1999). These birds are habitat specialists that exclusively breed in the mature Ashe juniper (*Juniperus ashei*)-oak (*Quercus* sp.) woodlands of the Edwards Plateau, where they use the shedding Ashe juniper bark for nest construction (Kroll 1980; Ladd and Gass 1999). A recent study found that the most suitable warbler habitat consists of 60-80% Ashe juniper woodlands with a high percentage of tree canopy cover and tree heights greater than 3 meters (Mueller et al. 2022). Similar studies have further suggested the importance of distance to forest edge on warbler density and seasonal productivity (Peak and Thompson 2013, Peak and Thompson 2014, Reidy et al. 2018). The mixed woodlands they inhabit are typically composed of Ashe juniper (*Juniperus ashei*), Texas red oak (*Quercus buckleyi*) and live oak (*Quercus fusiformis*) or other oak species depending on the region, all of which play roles in warbler ecology and behavior (Pulich 1976). Reidy et al. (2017) found that although the majority of studied nests were placed in junipers, nests were also located in live oaks, cedar elms, and shin oaks—21%, 8%, and 4%, respectively. Likewise, warbler foraging behavior is guided by phenology with foraging occurring on oak species early in the breeding season and switching to junipers in May (Marshall et al. 2013).

Currently, based on the Mueller et al. (2022) study, the breeding population of Golden-cheeked Warblers is predicted to have 217,444 males (95% CI = 153,917 - 311,965), although the authors note that this estimate applies most accurately at the regional scale and may provide slight overestimations in comparison to fine-scale local data. Other population estimates are significantly lower. Pulich (1976) estimated 14,750-18,486 pairs between 1962 and 1974, while Wahl et al. (1990) estimated 4,822-16,016 pairs from habitat analyses in the years 1974, 1976 and 1981. Although Mueller et al. (2022) estimated that the most suitable habitat can support ≥ 0.25 male warblers/ha, the majority of the predicted range wide abundance of this species occurs in areas with sub-optimal habitat that support fewer than 0.25 males/ha. Although the species was relatively common in 1982, the U.S. Fish & Wildlife Service (USFWS) petitioned to have it listed through an emergency listing in 1990 in response to land development and the habitat loss and degradation that would likely result in Travis County (USFWS 1990a). Extensive research has been conducted on habitat and biological characteristics of Golden-cheeked Warblers; however, research on the threat of climate change on warblers is limited. With the importance of Ashe juniper to both warbler foraging behavior and nest creation, assessing the impacts of climate change on junipers is essential to predicting whether suitable warbler habitat will shift or contract in distribution (Fuhlendorf 1996).

With climate change, the conditions that can lead to higher severity fire and drought have been increasingly more common (Fuhlendorf 1996, Reemts & Hansen 2008; Polley et al. 2018). With the additional impact of fire suppression, dense Ashe juniper-oak woodlands may face stand-replacing disturbances that could impact the availability and distribution of mature Ashe juniper (Reemts and Hansen 2008). Studies have found that Ashe juniper struggles to recolonize burned areas. Fuhlendorf et al. (1996) stated that juniper regeneration may take approximately 75 years. One longitudinal study found nearly no regeneration 24 years post crown fire, suggesting that fires reduce seed availability (Reemts and Hansen 2013, Reemts et al. 2024, Reidy et al. 2021). Drought has also been shown to have severe impacts on Ashe juniper-oak woodlands. In 2011, Texas experienced a massive tree mortality event after the worst drought on record, and in Central Texas, juniper-oak woodlands mortality was quite prevalent (Moore et al. 2016; Schwantes et al. 2017). A study found that juniper faced increased risk of mortality to this drought due to its slow growth and that because larger sized junipers grow more slowly, severe drought is expected to kill large numbers of tall, mature Ashe junipers (Polley et al. 2018). Therefore, as a slow growing, fire-sensitive species, the distribution of Ashe juniper is likely to be affected by climate-driven changes in fire regimes and drought severity, which are both intensified by increasing temperatures (Fuhlendorf et al. 1996, Harvey and Enright 2022).

To mitigate the effects of climate change on warbler populations, it is important to understand how climate change will affect the distribution of suitable habitat, especially its essential resource, Ashe juniper. Recent studies that used species distribution models (SDMs) to predict the effects of climate change on North American birds found that the Golden-cheeked Warbler could experience an expansion in breeding range by more than 25% (Bateman et al. 2020, Pham et al. 2022). Yet, these models do not account for certain species-specific traits that could affect the warbler from realizing the distribution expansion they suggest (Pham et al. 2022). Therefore, in this thesis, I explored how climate change will likely affect the distribution and relative abundance of the endangered Golden-cheeked Warbler via the distributional contraction of an essential resource, Ashe juniper.

In chapter 1, I investigated how climate change will potentially affect the distribution of Ashe juniper using an ensembled species distribution model (SDM). SDMs use historical environmental and climatic conditions data and species occurrence records and are often used to predict areas of potential suitability for species. SDMs have had a wide variety of applications including predicting invasive species impacts, modeling landscape connectivity and fire suitability, and projecting the potential effects of climate change (Stroh et al. 2018, Araujo et al. 2019, Naimi et al. 2022). In the last decade, with the advancement of computational and statistical methods, approaches for building SDMs have expanded (Zurell et al. 2020, Santini et al. 2021). Although many studies have projected climate-induced distribution shifts of flora and fauna, far fewer have explored how climate might alter the distribution of specific resources upon which a species depends. Doing so has the potential to help managers develop strategies and prioritize actions for resource-dependent at-risk species.

I used regression and machine learning-based algorithms to build an ensembled SDM for Ashe juniper. I then projected potential future distributions under four climate change scenarios based on the outputs of two generalized circulation models (GCMs) run for two shared socioeconomic pathways (SSPs). I then leveraged an existing warbler density model (Mueller et al. 2022) to isolate the persisting regions of warbler habitat based on the projected contractions of Ashe juniper.

In chapter 2, I used the projected changes in habitat developed in chapter 1 in an individual-based, spatially explicit, population model to simulate Golden-cheeked Warbler responses to climate-driven habitat change. Individual-based models (IBMs) can integrate landscape change and species traits to understand cumulative changes in population demography, movement, occupancy and persistence over time (DeAngelis and Grimm 2014). This mechanistic approach can allow practitioners to explore multiple scenarios that may include factors such as habitat change, disturbance, management, and adaptation to determine potential population responses and inform conservation strategies. I built a range-wide, spatially explicit IBM to simulate warbler responses to climate-induced resource loss with the purpose of determining the most important areas for the persistence of the species in the face of climate change. Because a vast majority of the warbler's range is owned by private landowners, protected areas, such as the Balcones Canyonlands Preserve (BCP) and the Balcones Canyonlands National Wildlife Refuge (BCNWR), have been essential in conserving breeding habitat and enforcing management plans for the species (Ladd and Gass 1999; Dreiss et al. 2022; Duarte et al. 2013). Therefore, an additional aim of this model was to assess the future of warbler occupancy within existing protected areas, as well as determine other potential climate refugia that could be prioritized for protection. My model can be used by researchers and practitioners to assess alternative scenarios at a broad spatial scale, or it can be fine-tuned to address more local management questions. This model contributes to the understanding of future Golden-cheeked Warbler population dynamics to inform landscape level conservation efforts of this at-risk species.

REFERENCES

Araújo, M. B., R. P. Anderson, A. Márcia Barbosa, C. M. Beale, C. F. Dormann, R. Early, R. A. Garcia, A. Guisan, L. Maiorano, B. Naimi, R. B. O’Hara, N. E. Zimmermann, and C. Rahbek. 2019. Standards for distribution models in biodiversity assessments. Science Advances 5:eaat4858.

Bateman, B. L., C. Wilsey, L. Taylor, J. Wu, G. S. LeBaron, and G. Langham. 2020. North American birds require mitigation and adaptation to reduce vulnerability to climate change. Conservation Science and Practice 2:e242.

Both, C., M. Van Asch, R. G. Bijlsma, A. B. Van Den Burg, and M. E. Visser. 2009. Climate change and unequal phenological changes across four trophic levels: constraints or adaptations? Journal of Animal Ecology 78:73–83.

Chapin III, F. S., E. S. Zavaleta, V. T. Eviner, R. L. Naylor, P. M. Vitousek, H. L. Reynolds, D. U. Hooper, S. Lavorel, O. E. Sala, S. E. Hobbie, M. C. Mack, and S. Díaz. 2000. Consequences of changing biodiversity. Nature 405:234–242.

DeAngelis, D. L., and V. Grimm. 2014. Individual-based models in ecology after four decades. F1000Prime Reports 6:39.

Dreiss, L., P. Sanchez-Navarro, and B. Bird. 2022. Spatiotemporal patterns in Golden-cheeked Warbler breeding habitat quantity and suitability. Avian Conservation and Ecology 17:art14.

Duarte, A., J. L. R. Jensen, J. S. Hatfield, and F. W. Weckerly. 2013. Spatiotemporal variation in range-wide Golden-cheeked Warbler breeding habitat. Ecosphere 4:1–12.

Fuhlendorf, S. D., F. E. Smeins, and W. E. Grant. 1996. Simulation of a fire-sensitive ecological threshold: a case study of Ashe juniper on the Edwards Plateau of Texas, USA. Ecological Modelling 90:245–255.

Harvey, B. J., and N. J. Enright. 2022. Climate change and altered fire regimes: impacts on plant populations, species, and ecosystems in both hemispheres. Plant Ecology 223:699–709.

Hitch, A. T., and P. L. Leberg. 2007. Breeding Distributions of North American Bird Species Moving North as a Result of Climate Change. Conservation Biology 21:534–539.

Kroll, J. C. 1980. Habitat Requirements of the Golden-Cheeked Warbler: Management Implications. Journal of Range Management 33:60.

Ladd, C., and L. Gass. 1999. Golden-cheeked Warbler (Setophaga chrysoparia), version 1.0. Birds of the World.

Littlefield, C. E., M. Krosby, J. L. Michalak, and J. J. Lawler. 2019. Connectivity for species on the move: supporting climate-driven range shifts. Frontiers in Ecology and the Environment 17:270–278.

Marshall, M. E., M. L. Morrison, and R. N. Wilkins. 2013. Tree Species Composition and Food Availability Affect Productivity of an Endangered Species: The Golden-Cheeked Warbler. The Condor 115:882–892.

Moore, G. W., C. B. Edgar, J. G. Vogel, R. A. Washington-Allen, R. G. March, and R. Zehnder. 2016. Tree mortality from an exceptional drought spanning mesic to semiarid ecoregions. Ecological Applications 26:602–611.

Mueller, J. M., S. E. Sesnie, S. E. Lehnen, H. T. Davis, J. J. Giocomo, J. N. Macey, and A. M. Long. 2022. Multi-scale species density model for conserving an endangered songbird. The Journal of Wildlife Management 86:e22236.

Naimi, B., C. Capinha, J. Ribeiro, C. Rahbek, D. Strubbe, L. Reino, and M. B. Araújo. 2022. Potential for invasion of traded birds under climate and land-cover change. Global Change Biology 28:5654–5666.

Peak, R. G., and F. R. Thompson III. 2013. Amount and Type of Forest Cover and Edge are Important Predictors of Golden-Cheeked Warbler Density. The Condor 115:659–668.

Peak, R. G., and F. R. Thompson III. 2014. Seasonal productivity and nest survival of Golden-cheeked Warblers vary with forest type and edge density. The Condor 116:546–559.

Pham, C. H., J. J. Price, J. M. Tallant, and D. N. Karowe. 2022. Climate change is predicted to reduce sympatry among North American wood-warblers. Ornithological Applications 124:duac025.

Polley, H. W., D. M. Johnson, and R. B. Jackson. 2018. Projected drought effects on the demography of Ashe juniper populations inferred from remote measurements of tree canopies. Plant Ecology 219:1259–1267.

Portalier, S. M. J., J.-N. Candau, and F. Lutscher. 2022. A temperature-driven model of phenological mismatch provides insights into the potential impacts of climate change on consumer–resource interactions. Ecography 2022:e06259.

Pulich, W. M. 1976. Review of The Golden-Cheeked Warbler. The Auk 94:799–801.

Reemts, C. M., and L. L. Hansen. 2008. Slow recolonization of burned oak–juniper woodlands by Ashe juniper (Juniperus ashei): Ten years of succession after crown fire. Forest Ecology and Management 255:1057–1066.

Reemts, C. M., and L. L. Hansen. 2013. Short-Term Effects of Repeated Wildfires in Oak-Juniper Woodlands. Fire Ecology 9:64–79.

Reemts, C. M., C. Picinich, and J. H. Sperry. 2024. Crown fires remove a fire-sensitive canopy dominant from oak-juniper woodlands: results from long-term monitoring of wildfires. Fire Ecology 20:73.

Reidy, J. L., F. R. Thompson III, G. M. Connette, and L. O'Donnell. 2018. Demographic rates of Golden-cheeked Warblers in an urbanizing woodland preserve. The Condor 120:249–264.

Reidy, J. L., F. R. Thompson, S. Rowin, C. Schwope, and J. M. Mueller. 2021. Effects of prescribed fire on fuels, vegetation, and Golden-cheeked warbler (*Setophaga chrysoparia*) demographics in Texas juniper-oak woodlands: An update six years post-fire. Forest Ecology and Management 492:119191.

Reidy, J. L., F. R. Thompson III, and L. O'Donnell. 2017. Density and nest survival of golden-cheeked warblers: Spatial scale matters. The Journal of Wildlife Management 81:678–689.

Román-Palacios, C., and J. J. Wiens. 2020. Recent responses to climate change reveal the drivers of species extinction and survival. Proceedings of the National Academy of Sciences of the United States of America 117:4211–4217.

Santini, L., A. Benítez-López, L. Maiorano, M. Čengić, and M. A. J. Huijbregts. 2021. Assessing the reliability of species distribution projections in climate change research. Diversity and Distributions 27:1035–1050.

Schumaker, N. H., and A. Brookes. 2018. HexSim: a modeling environment for ecology and conservation. Landscape ecology 33:197–211.

Schwantes, A. M., J. J. Swenson, M. González-Roglich, D. M. Johnson, J.-C. Domec, and R. B. Jackson. 2017. Measuring canopy loss and climatic thresholds from an extreme drought along a fivefold precipitation gradient across Texas. Global Change Biology 23:5120–5135.

Stambaugh, M. C., G. Creacy, J. Sparks, and M. Rooney. 2017. Three centuries of fire and forest vegetation transitions preceding Texas' most destructive wildfire: Lost Pines or lost oaks? Forest Ecology and Management 396:91–101.

Stambaugh, M. C., J. C. Sparks, and E. R. Abadir. 2014. Historical Pyrogeography of Texas, USA. Fire Ecology 10:72–89.

Stroh, E. D., M. A. Struckhoff, M. C. Stambaugh, and R. P. Guyette. 2018. Fire and Climate Suitability for Woody Vegetation Communities in the South Central United States. Fire Ecology 14:106–124.

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

Twining, C. W., J. R. Shipley, and B. Matthews. 2022. Climate change creates nutritional phenological mismatches. Trends in Ecology & Evolution 37:736–739.

U.S. Fish and Wildlife Service [USFWS]. 1990a. Endangered and threatened wildlife and plants—emergency rule to list the golden-cheeked warbler as endangered. Federal Register 55:18844–18845

Urban, M. C. 2015. Accelerating extinction risk from climate change. Science 348:571–573.

Wahl, R., D. D. Diamond, and D. Shaw. 1990. The golden-cheeked warbler: a status review. Austin, Texas, USA.

Wilkening, J., W. Pearson-Prestera, N. A. Mungi, and S. Bhattacharyya. 2019. Endangered species management and climate change: When habitat conservation becomes a moving target. Wildlife Society Bulletin 43:11–20.

Zurell, D., J. Franklin, C. König, P. J. Bouchet, C. F. Dormann, J. Elith, G. Fandos, X. Feng, G. Guillera-Arroita, A. Guisan, J. J. Lahoz-Monfort, P. J. Leitão, D. S. Park, A. T. Peterson, G. Rapacciuolo, D. R. Schmatz, B. Schröder, J. M. Serra-Diaz, W. Thuiller, K. L. Yates, N. E. Zimmermann, and C. Merow. 2020. A standard protocol for reporting species distribution models. Ecography 43:1261–1277.

CHAPTER 1.

RESEARCH ARTICLE

Potential impacts of climate-driven Ashe juniper (*Juniperus ashei*) range contraction on Golden-cheeked Warbler (*Setophaga chrysoparia*) habitat.

Leticia Santillana Fernandez[1*], Joshua J. Lawler[1], and Julie A. Heinrichs[2]

[1]School of Environmental and Forest Sciences, University of Washington, Seattle, Washington, USA

[2]Computational Ecology Group Inc., Canmore, Alberta, Canada

*Corresponding author: letysf18@uw.edu

ABSTRACT

Climate change is likely to have cascading effects on species through changes to their habitats, food, and other resources. For at-risk birds, climate-change impacts on specific plant species could result in a significant reduction in habitat, possibly leading to population declines or even extinctions. The endangered *Setophaga chrysoparia* (Golden-cheeked Warbler), which relies on the bark of mature *Juniperus ashei* (Ashe juniper) for nest construction may be one of these bird species. We combined juniper occurrence records with environmental, topographic, and edaphic variables to generate an ensembled species distribution model to project the potential future distribution of *J. ashei*. We then used four different climate-change scenarios to project changes in *J. ashei* distribution within the range of *S. chrysoparia* for the years 2040, 2060, 2080, and 2100. We then used the projected *J. ashei* distributions in conjunction with an existing *S. chrysoparia* density model (Mueller et al. 2022) to assess potential changes in *S.*

chrysoparia habitat availability. The three most important variables in the ensembled model for projecting the presence of *J. ashei* were mean diurnal temperature range, precipitation of warmest quarter, and available water storage in the top 100 cm of soil. Contractions in the distribution of *J. ashei* varied from 70% to 99% within the study area by 2100. These range contractions translated into a reduction in the amount of optimal and marginal *S. chrysoparia* habitat by up to 1,026 km^2 (-92%) and 9,484.6 km^2 (-78%), respectively. Our results provide an indication of the impact climate change could have on an essential resource for the endangered *S. chrysoparia*, and the spatial patterns our models predict could help managers target habitat protection and restoration efforts where *J. ashei* suitability is projected to persist.

Keywords: Ashe juniper, climate change projections, distribution, endangered species, golden-cheeked warbler, habitat, Juniperus ashei, Setophaga chrysoparia

Predicción del impacto del cambio climático en la distribución del enebro de frutos azules (*Juniperus ashei*): Implicaciones de la perdida de recursos para la reinita caridorada (*Setophaga chrysoparia*)

RESUMEN

El cambio climático probablemente tendrá efectos en cascada en las especies a través de cambios en sus hábitats, alimentos, y otros recursos. Para las aves en riesgo de extinción, los impactos del cambio climático en especies de plantas necesitadas podrían resultar en una reducción significativa de su hábitat, posiblemente resultando en disminuciones de población o incluso extinciones. La especie en peligro de extinción *Setophaga chrysoparia* (reinita caridorada), que depende de la corteza de *Juniperus ashei* (enebro de frutas azules) maduro para la construcción de nidos, puede ser una de estas especies de aves. Combinamos registros de presencia de *J. ashei* con variables ambientales, topográficas, y edáficas para generar un modelo de distribución de especies ensamblado con el fin de proyectar la posible distribución futura de *J. ashei*. Despues, usamos cuatro escenarios diferentes de cambio climático para proyectar cambios en la distribución de *J. ashei* dentro del rango de *S. chrysoparia* para los años 2040, 2060, 2080, y 2100. Posteriormente, utilizamos las distribuciones proyectadas de *J. ashei* junto con una modelo de densidad de *S. chrysoparia* (Mueller et al. 2022) para evaluar los posibles cambios en la disponibilidad de hábitat de *S. chrysoparia.* Las tres variables más importantes en el modelo ensamblado para proyectar la presencia de *J. ashei* fueron el promedio del rango de temperatura diurna, la precipitación del trimestre más cálido, y el almacenamiento de agua en los primeros 100 cm del suelo. Las contracciones en la distribución de *J. ashei* variaron del 70% al 99% dentro del área del estudio para el año 2100. Estas contracciones de rango se tradujeron en una reducción en la cantidad de hábitat optimo y marginal de *S. chrysoparia* de hasta 1,026 km^2 (-92%) y 9,484.6 km^2 (-78%), respectivamente. Nuestros resultados proporcionan una indicación del impacto que el cambio climático podría tener en un recurso esencial para *S. chrysoparia*, y los patrones espaciales que predicen nuestros modelos podrían ayudar a los gestores a dirigir los esfuerzos de protección y restauración del hábitat donde se proyecta que la idoneidad de *J. ashei* persista.

Palabras clave: distribución, enebro de frutas azules, especies en peligro de extinción, hábitat, Juniperus ashei, proyecciones del cambio climático, reinita caridorada, Setophaga chrysoparia

LAY SUMMARY

- We used multiple models to explore how climate change could impact Golden-cheeked Warbler habitat through its effect on the distribution of Ashe juniper.

- Under the most extreme climate scenario, the distribution of Ashe juniper could experience a 99% contraction by 2100.
- Although there are always uncertainties in climate-impact projections, the magnitude of some of the projected juniper range contractions presented here could lead to the extinction of the Golden-cheeked Warbler in Texas.

INTRODUCTION

Anthropogenic climate change poses a major threat to global biodiversity, with rapid shifts in environmental and climatic conditions affecting ecological processes, phenology, and habitat configuration (Urban 2015, Portalier et al. 2022). In forested areas, increases in the frequency of extreme heat and chronic exposure to high temperatures are leading to drought-related stress and tree mortality, as well as higher risk of severe wildfires (Harvey & Enright 2022). These shifts in climatic patterns and disturbance regimes affect tree and vegetation regeneration and ecosystem function, which can result in disruptions of interspecific interactions and limit species persistence (Harvey & Enright 2022, Twinning et al. 2022). Increases in maximum annual temperatures have been found to be one of the most important factors in local extinctions, especially when species do not increase their historical dispersal rates to follow climatic shifts. Birds that depend on forested landscapes may not be able to adapt to changing vegetation structure and composition if the shifts happen too quickly or in unexpected ways. Hitch and Leberg (2007) found that some bird species that are capable of tracking these changes have shifted their distributions northward. However, for highly specialized species, distributional shifts or adaptation to new resources may not be quick enough to prevent extinction (Portalier et al. 2022).

As an endangered habitat specialist, *Setophaga chrysoparia* (Golden-cheeked Warbler) is an example of a species that has faced extensive habitat loss and fragmentation, leaving it particularly vulnerable to climate change (USFWS 1990a). *S. chrysoparia* underwent an emergency listing in 1990 as a result of increased urbanization in central Texas. *S. chrysoparia* exclusively breeds in the Ashe juniper (*Juniperus ashei)*-oak (*Quercus spp.*) woodlands of central Texas and depends on the stringy bark of mature junipers for nest construction, which limits the capacity of this species to adapt to a changing landscape (Pulich 1976, Ladd and Gass 1999). In addition to the shedding bark of *J. ashei*, *S. chrysoparia* habitat requirements also include structural components such as 60-80% juniper cover, high percent canopy cover, and juniper trees taller than 3 meters (Mueller et al. 2022). Warblers tend to use several different oak species in proximity to juniper, where they procure nest building materials (Marshall et al. 2013). Such species include Texas red oak (*Quercus buckleyi*) or post oak (*Quercus stellata*). Given their ability to use several species of oak, a change in the distribution of any one oak species might have relatively little impact on warbler habitat. By contrast, any reduction of mature *J. ashei* would likely lead to major changes in warbler distribution and density (Marshall et al. 2013, Van Auken et al. 2023).

With increases in extreme temperatures and changes in weather patterns, harsh drought conditions and severe crown fires have increased tree mortality of young and mature Ashe junipers, further reducing warbler habitat (Johnson et al. 2018, Crouchet et al. 2019, Reemts et al. 2024, Reidy et al. 2021). Despite *J. ashei* being a relatively drought tolerant species, in the 2011-2013 Texas drought, mortality was prevalent for junipers with the slowest growth rates and those in deeper soils where bedrock water storage was not accessible (Polley et al. 2016, Crouchet et al. 2019, Schwantes et al. 2016, 2017). In the Edwards Plateau, juniper populations experienced a 27% canopy dieback following the 2011-2013 drought (Johnston et al. 2018). Schwantes et al. (2018) also projected a high amount of dynamic water stress through the 21st century that could lead to increased juniper mortality. In savannas, drought led to high mortality risk in larger trees, urging researchers to warn of a potential shift in the size distribution of the species (Polley et al. 2018). Furthermore, under climate change, the conditions that can lead to drought-related tree mortality and high severity fires (extreme heat and high fuel loads) have been steadily increasing in the central region of the United States (Reemts & Hansen 2008, Polley et al. 2018, Gao et al. 2021, Nielson-Gammon et al. 2021). Despite extensive research to understand the impacts of prescribed fire and drought on juniper-oak woodlands, the extent to which climate change will affect the geographical distribution of *J. ashei* is still unclear.

Here, we explore the potential impact of climate-induced resource loss on *S. chrysoparia* using a combination of a species distribution model (SDM) and an existing warbler density model (Mueller et al. 2022). First, we built a weighted ensembled SDM for *J. ashei* and projected the species' potential geographic distributions through 2100 using projections from two generalized circulation models (GCMs) run for two shared socioeconomic pathways (SSPs). We then used the projected *J. ashei* distributions to restrict the availability of marginal and optimal *S. chrysoparia* habitat as determined by an existing warbler density model (Mueller et al. 2022). This work will highlight the implications of resource loss and determine the regions of conservation concern that could inform the management of the endangered *S. chrysoparia*.

METHODS

Species Data

J. ashei is a non-resprouting, evergreen tree that can be found throughout central Texas and in certain parts of Oklahoma, Arkansas, Missouri and Mexico (Johnsen and Alexander 1974, Pulich 1976). This tree is typically distributed along Cretaceous limestone and shallow soils (Diamond 1997). Within Texas, Ashe juniper forms an important part of diverse plant communities across the Edwards Plateau, Cross-Timbers and Post Oak Savannah ecoregions, yet the communities associated with the most suitable warbler habitat are restricted primarily to the Edwards Plateau (Griffith et al. 2007). Although a few records exist in northern Mexico, the data used for model building was constrained to records within the United States due to the lack of comparable data for our selected edaphic variables in Mexico (Figure 1.1). Additionally, we constrained the projections of future distributions to within Texas because our intent was to assess changes within the current breeding range of *S. chrysoparia*. The presence of agriculture in the states north of Texas, increased urbanization, and the edaphic and topographic constraints that create suitable conditions for *J. ashei* further limit the possibility of a northward expansion that would follow any associated climatic conditions. Furthermore, because under no scenario did our model project an expansion of the range of *J. ashei* within Texas or Oklahoma, we did not feel it necessary to reconsider our original plan to focus on the existing warbler distribution.

Occurrence data for *J. ashei* were extracted from the Global Biodiversity Information Repository using the "*rgbif*" package in R (Chamberlain et al. 2024, GBIF, https://www.gbif.org/, accessed in March 2024). These data were filtered to remove any records with geospatial issues as well as any records of fossil and living specimens (e.g. botanical gardens, museum collections). We filtered our occurrence data to include only records from

1960-2010 to increase the predictive accuracy of the models. As a long-lived tree species in a fire suppressed landscape, we assumed that any records between 1960 and 2010 would be representative of individuals in the landscape within the 1970-2000 timeframe of the historical climate data. To reduce the spatial bias of record collection, the data was spatially thinned using "*spThin*" in RStudio to ensure no points were within 5 km of each other, resulting in 165 records (Aiello-Lammens et al. 2015). 20% of these records were then left out for ensemble-model validation, leaving 132 records for model building. All data preparation, modeling and predictions were developed using R 4.4.1 (R Core Team 2024).

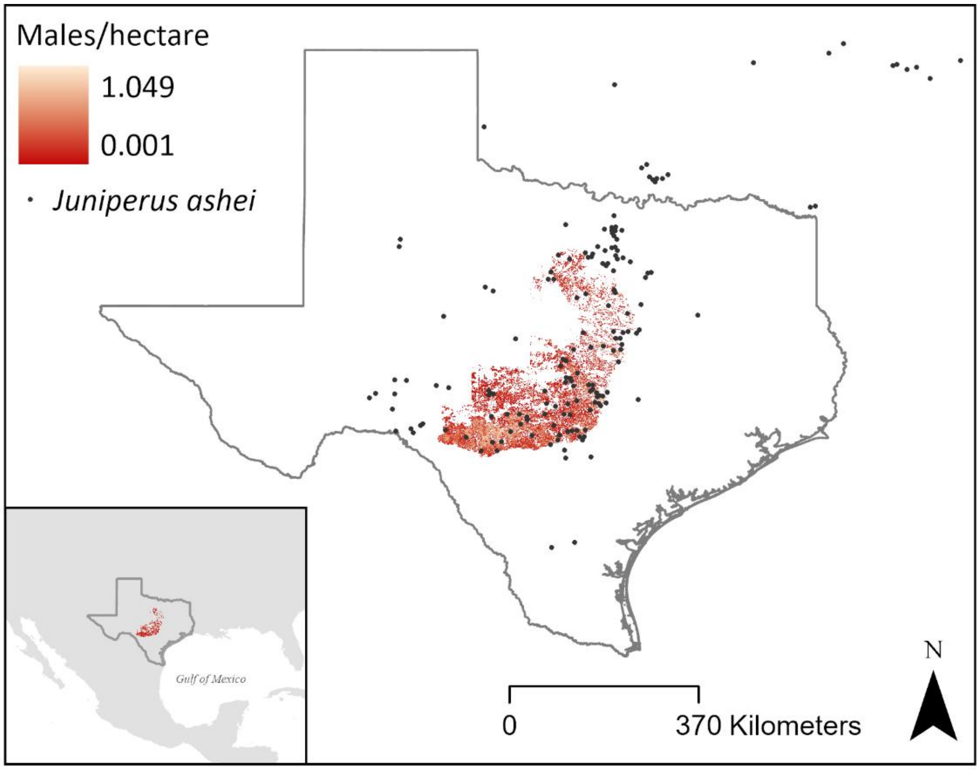

Figure 1.1 *J. ashei* occurrence records from the Global Biodiversity Information Facility (GBIF) that were used for creating the species distribution model. *S. chrysoparia* density model is shown for spatial reference (Mueller et al. 2022).

Environmental Covariates

J. ashei persists in arid and semi-arid conditions. However, research has found that crown mortality can be affected by soil moisture, soil depth, extreme heat, and drought (Diamond 1997, Polley et al. 2016, Crouchet et al. 2019). Thus, we used a set of environmental covariates that included climatic, topographic, and edaphic variables. Historical bioclimatic predictors at a spatial resolution of 30 arc-seconds (~1-km) were downloaded from the WorldClim-Global Climate Database 2.1 (Fick and Hijmans 2017; available at https://worldclim.org/) (Table 1.1).

The downscaled future climate projections were downloaded from the WorldClim Coupled Model Intercomparison Project 6 (CMIP6) database associated with the 6th IPCC Assessment Report (available at https://www.worldclim.org/). We downloaded a total of four climate-change scenarios from two GCMs under two SSP scenarios. Data for the SSP2-4.5 and SSP3-7.0 scenarios was used for four time periods: 2021-2040, 2041-2060, 2061-2080, and 2081-2100. SSP2-4.5 is considered a middle-of-the-road scenario in which humanity aims to limit warming to approximately 3˚C by 2100. To provide a slightly more extreme future climate, SSP3-7.0, known as Regional Rivalry, is similar to SSP2-4.5 but with increased land-use change and high aerosol emissions (O'Neill et al. 2016). The GCMs for these SSPs were selected using the *GCMeval* tool to capture a range of future climates for Texas (Parding et al. 2020). *GCMeval* works by ranking models based on user-selected weights on relevant variables (e.g., region, season, temperature). We selected central North America as the most important focus region, and prioritized spring and summer seasons over the rest of the settings. We originally selected other more highly ranked GCMs, however, some data were not yet available in the WorldClim database. The ranked models we selected were the Max Planck Institute Earth System Model (MPI-ESM1-2-HR) and the U.K. Earth System Model (UKESM1-0-LL) (Gutjahr et al. 2019, Yukimoto et al. 2019, Sellar et al. 2019). UKESM1-0-LL was chosen for forecasting a large increase in temperature and precipitation while MPI-ESM1-2-HR represents a minimal change in precipitation with a modest temperature increase (Table 1.1).

Table 1.1 Selected variables for model building for historic climate (1970-2000) and for the last time period (2081-2100) for future climate scenarios. Three other relevant variables are included for comparison.

Variable	**Historic**	**MPI-ESM1-2-HR**		**UKESM1**	
		SSP2-4.5	**SSP3-7.0**	**SSP2-4.5**	**SSP3-7.0**
Mean diurnal range (˚C)	13.7 ± 1.7	13.6 ± 1.8	13.6 ± 1.7	13.9 ±1.8	13.7 ±1.8
Temperature seasonality (˚C)	786.7 ± 96.2	787.6 ± 108.7	813.9 ± 115.6	787.8 ± 101.0	810.0 ± 108.7
Max. temp. of the warmest month (˚C)	34.3 ± 1.24	36.3 ± 1.5	37.9 ± 1.4	38.8 ± 1.2	40.8 ± 1.3
Mean temp. of the wettest quarter (˚C)	21.5 ± 4.3	24.2 ± 5.5	25.8 ± 4.6	24.9 ± 5.5	26.1 ± 5.6
Precipitation of warmest quarter (mm)	227.4 ± 64.6	229.3 ± 82.1	211.1 ± 77.4	227.8 ± 52.6	213 ± 42.8
Topographic ruggedness index (m)	1.1 ± 1.4 (static)				
Topographic position index	-0.0 ± 0.5 (static)				
Topographic wetness index	8.96 ± 1.7 (static)				
Available water storage (mm)	107.1 ± 41.0 (static)				
Soil organic carbon (g C/m^2)	5815.7 ± 3909.2 (static)				

A digital elevation model (DEM) at a spatial resolution of 1 arc-second (~30 m in the study region) was downloaded from the U.S. Geological Survey Lidar Explorer database and processed with the "*terra*" package in the R statistical environment to calculate slope, terrain ruggedness index (TRI), and topographic position index (TPI) (Hijmans et al. 2024, U.S. Geological Survey 2019). We also calculated topographic wetness index (TWI) in ArcGIS Pro using the same DEM data due to the importance of soil moisture on tree mortality (Kopecky et al. 2021, Schwantes et al. 2018). Categorical edaphic covariates were extracted at a 30-meter resolution from the gSSURGO database via ArcMap, which included available water storage and soil organic carbon, both at the root zone (0-100cm) (Peters et al. 2013, Soil Survey Staff; accessed on January 15, 2024). The soil layers were then transformed into numerical rasters using the "*rasterDT*" package in RStudio (O'Brien 2022). Topographic and soil data were resampled to match the spatial resolution of the bioclimatic data (1-km).

To address any potential multicollinearity issues, environmentally relevant covariates were chosen followed by a sequential dropping of variables with a Variance Inflation Factor (VIF) greater than four (Zuur et al. 2010). This was accomplished using the "*usdm*" package in RStudio (Naimi 2023). We further confirmed the low correlation among selected covariates using Pearson's correlation coefficient. The variable selection process led to the inclusion of only 9 of the 25 variables for modeling: 1) mean diurnal temperature range (bio2), 2) temperature seasonality (bio4), 3) maximum temperature of the warmest month (bio5), 4) mean temperature of the wettest quarter (bio8), 5) precipitation of warmest quarter (bio18), 6) topographic ruggedness index, 7) topographic position index, 8) topographic wetness index, 9) available water storage, and 10) soil organic carbon. The averages for each of the variables within the modeling area were calculated for the historical (1970-2000) and the end-of-century time period (2081-2100) for each of the four climate scenarios (Table 1.1).

Species Distribution Modeling (SDM)

We built the species distribution model for *J. ashei* using the "*sdm*" package in R (Naimi and Araújo 2016). Due to the lack of absence data, randomly selected background points were used for model fitting. We ran multiple models using different numbers of background points. The most efficient and best performing models used 10,000 background points, which matched previous research findings on the ratio between presence and background points (Barbet-Massin et al. 2012). To build an ensemble that incorporated regression and tree-based methods, we used random forests (RF), maxNet, boosted regression trees (BRT), and generalized additive models (GAM) algorithms. After testing different settings for parameterization and computational efficiency, we settled on using the standard settings for the four algorithms based on model performance. Each of the algorithms was replicated ten times using a k-fold cross-validation resampling approach (k = 10), which calibrated and evaluated the models with 30% of the data in each replicate (Hijmans 2012). To evaluate the performance of each model, we first used the threshold-independent area under the curve (AUC) and threshold-dependent True Skills Statistic (TSS), where AUC values closer to 1 and TSS values higher than 0.40 were assumed to indicate good model performance (Ahmad et al. 2019). Additionally, the Boyce Index, which is a preferred model evaluation metric for presence-only models, was calculated using the "*ecospat*" package in R (Boyce et al. 2002, Hirzel et al. 2006, Di Cola et al. 2016). This index is calculated using a Spearman correlation of the plot of the predicted to expected ratio along a gradient of suitability values. The closer the Boyce Index is to +1 the more the evaluation data agrees with model predictions.

We built a weighted ensemble by scaling replicate predictions based on the value of TSS, which is calculated for each model to assess predictive performance (Hao et al. 2019). To evaluate the performance of the ensemble model, we validated the predicted raster with the 20% of *J. ashei* records that were not used for training the models. The final weighted ensemble model was then used to project the historical and future distribution of *J. ashei*.

Predicted Warbler Distribution

We used the ensemble model to project potential future distributions of Ashe juniper for each of the four climate projections and four time periods. We created a binary variable from the continuous predicted values using a threshold that maximized the specificity and sensitivity of the TSS metric. We then resampled the resulting binary maps to a 10-meter resolution to match the Mueller et al. (2022) *S. chrysoparia* density model. This model, which estimates male densities throughout the breeding range as a function of relevant predictors such as canopy cover and percent *J. ashei* cover, was stratified using Mueller et al.'s defined habitat categories: low (0.001-0.0625 males/ha), marginal (0.0625-0.25 males/ha), and optimal (≥0.25 males/ha). We decided to focus on determining the impact of climate change on marginal and optimal quality habitat due to the limited research on the use of low-quality habitat. The categorized raster of density-based *S. chrysoparia* habitat was clipped by the binarized *J. ashei* projections for all future scenarios to represent any loss of habitat resulting from changes in the distribution of *J. ashei*. We calculated the difference in the amount of habitat identified by the Mueller et al. (2022) model for all scenarios and time periods to determine the extent of climate-induced habitat change. Because the rasters were projected in meters, pixel distortion did not have to be considered for these calculations and did not appear to make a significant difference in the area calculation for the high computational demand required for each calculation.

RESULTS

J. ashei Species Distribution Model

AUC values for the individual algorithms were all greater than 0.84 and TSS values were greater than 0.61. Model averaging through a weighting that maximized specificity and sensitivity for the TSS metric resulted in a TSS value was 0.8369 showing a high degree of discrimination between presence and expected absence. We used a TSS-based threshold of 0.1854 to binarize the ensembled model predictions. For the ensemble model, the Boyce Index value was 0.977 using the Spearman method, indicating high predictive performance for the weighted ensemble.

Variable importance was also calculated for the ensembled model through a weighted mean based on the TSS metric. Based on both the Pearson correlation and AUC metric, the three most important variables for determining the presence of *J. ashei* were mean diurnal temperature range (bio2, 39.5%), precipitation of warmest quarter (bio18, 32.9%) and available water storage in the top 100 cm of soil (29.8%). The model shows that *J. ashei* is most likely to be present when the precipitation of the warmest quarter remains between 100-200 mm and when the mean diurnal temperature range is below 12˚C. The probability of *J. ashei* presence decreased with increasing available water storage in a nearly linear fashion, which is most likely due to the species existing mainly on limestone outcrops and shallow soils.

Current predicted distribution of *J. ashei*.

Our projected distribution of *J. ashei* under historical climate (1970-2000) is similar to that produced by previous abundance and distribution models (e.g., Gray et al. 2012, Hargrove 2016). The probabilities of suitable conditions for *J. ashei* existing based on historical climate data (1970-2000) ranged from 0.2% to 60.1% probability of presence (Figure 1.2). The area projected to have occurrences based on the binary classification of the projected values covers 90,940 km^2 and is contained mainly within the Edwards Plateau, Post Oak Savannah, and Cross-Timber's ecoregions of central Texas, as well as the southernmost part of Oklahoma. However, within the breeding range of *S. chrysoparia*, the average probability of suitable conditions for *J. ashei* under the historical climate was only 0.26 ± 0.068 (range: 0.017-0.6) with the most suitable areas existing in the southeastern edge of the Edwards Plateau (Figure 1.2 and 1.3).

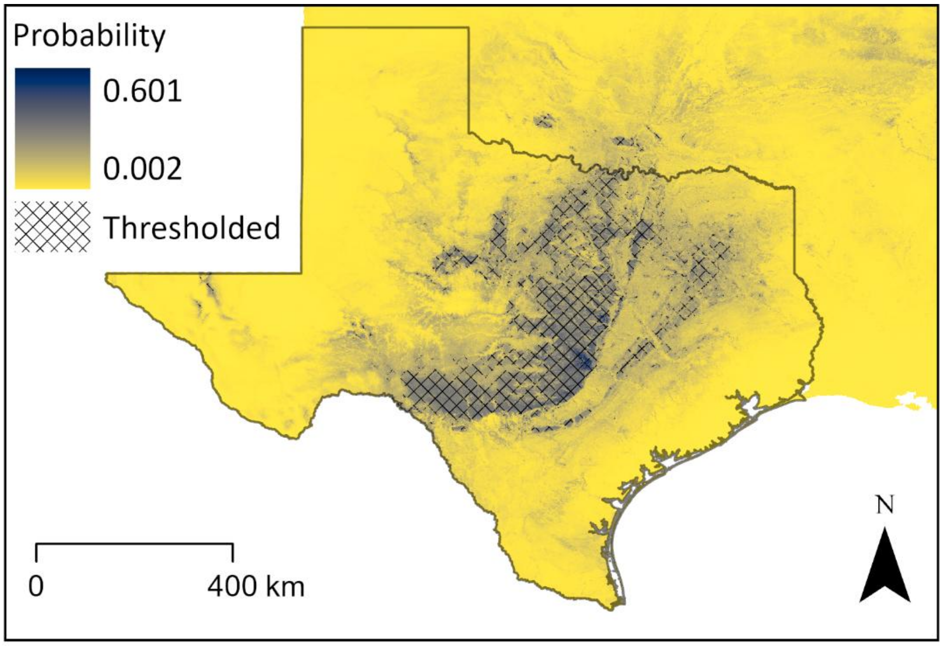

Figure 1.2 Modeled probability of *J. ashei*-associated environmental conditions under historical climate (1970-2000) within the modeling area. Hashed area shows the most probable area based on an applied threshold calculated from a weighted average of all models that maximized specificity and sensitivity of the TSS metric.

Future projected *J. ashei* distributions.

The ensembled species distribution model was applied to four future climate scenarios. All scenarios resulted in a projected reduction in suitability by 2100 across the modeling extent. Additionally, the southernmost edge of the *S. chrysoparia* range is where the highest probabilities of *J. ashei* occurrence remain across all scenarios, highlighting a potential focus on protecting the species in this region. As the climate scenarios become more distinct from historical conditions, the distribution of *J. ashei* occurrence probabilities become increasingly dense between 0 and 0.2 (Figure 1.3 and 1.4).

From the 90,940 km^2 of suitable *J. ashei* conditions in the historical scenario, the binarized projections from the MPI-ESM1-2-HR model resulted in a 70% decrease in the suitable area under SSP2-4.5 (27,681 km^2 remaining) and a 93% decrease under SSP3-7.0 (6,580 km^2 remaining) by the 2081-2100 time period (Table 2). For this GCM under SSP2-4.5, the distribution of suitable conditions for *J. ashei* remain throughout the majority of the Edwards Plateau and the Cross-Timbers ecoregions, but by the 2081-2100 time period, the suitability within the Post Oak Savannah nearly disappears in its southern edge. However, under the SSP3-7.0 scenario, by 2100, the suitability within the Cross-Timbers and Post Oak Savannah ecoregions disappears entirely and only the southern region of the Edwards Plateau remains suitable. Within the *S. chrysoparia* breeding range, the MPI-ESM1-2-HR model under the SSP2-4.5 predicts the most suitable conditions for *J. ashei* for all time periods with the period 2081-2100 reflecting an average probability of occurrence of 0.18 ± 0.071 (range: 0.0054 -0.43), which is still a significant reduction from the historical average of 0.26 ± 0.068 (range: 0.017-0.6) (Figure 1.3 and 1.4).

For the climate projections from the UKESM1-0-LL model, the distribution of suitable conditions for *J. ashei* is reduced by at least 83% in the first time period (2021-2040) and by the last time period (2081-2100), *J. ashei* disappears almost entirely in the three main ecoregions with isolated regions of suitability existing in the southeastern part of the Edwards Plateau ecoregion. The suitable area decreased by approximately 99% for both SSP2-4.5 (888 km^2 remaining) and SSP3-7.0 (646 km^2 remaining) (Table 1.2). Under the most extreme scenario, UKESM1-0-LL SSP3-7.0, the average probability of occurrence within the *S. chrysoparia* breeding range is largely reduced to 0.076 ± 0.04 (range: 0.003-0.279) for the period 2081-2100 (Figure 1.3 and 1.4).

Table 1.2 Expanse variation (in km^2 and %) of the threshold-based suitable habitat of *J. ashei* under four future climate scenarios in relation to the historic period of 1970-2000.

Time Period	**Historical**	**MPI-ESM1-2-HR**		**UKESM1**	
		SSP2-4.5	SSP3-7.0	SSP2-4.5	SSP3-7.0
1970-2000	90,940 (100%)	-	-	-	-
2021-2040	-	45,228 (-50.3%)	50,420 (-44.6%)	15,442 (-83%)	12,667 (-86%)
2041-2060	-	39,928 (-56.1%)	35,558 (-60.9%)	3,997 (-95.6%)	3,588 (-96%)
2061-2080	-	31,224 (-65.7%)	17,068 (-81.2%)	1,589 (-98.3%)	1,291 (-98.6%)
2081-2100	-	27,681 (-69.7%)	6,580 (-93%)	888 (-99%)	646 (-99.3%)

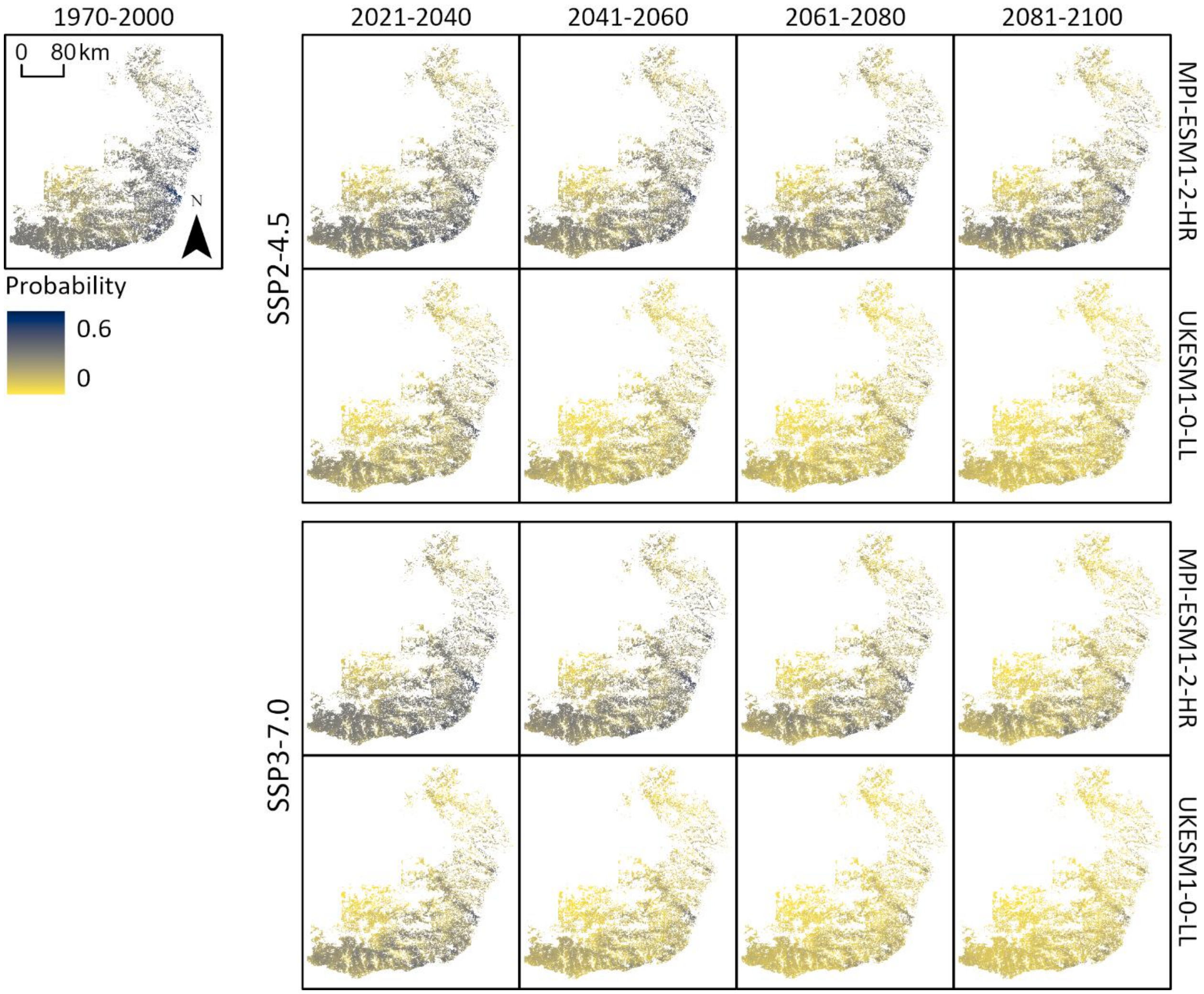

Figure 1.3 Probability of *Juniperus ashei*-associated environmental conditions remaining suitable through 2100. Conditions were modeled under SSP2-4.5 and SSP3-7.0 for two generalized circulation models. Results show that, under the majority of the climate scenarios, the suitability for *J. ashei* is expected to decrease drastically by 2100, especially under SSP3-7.0.

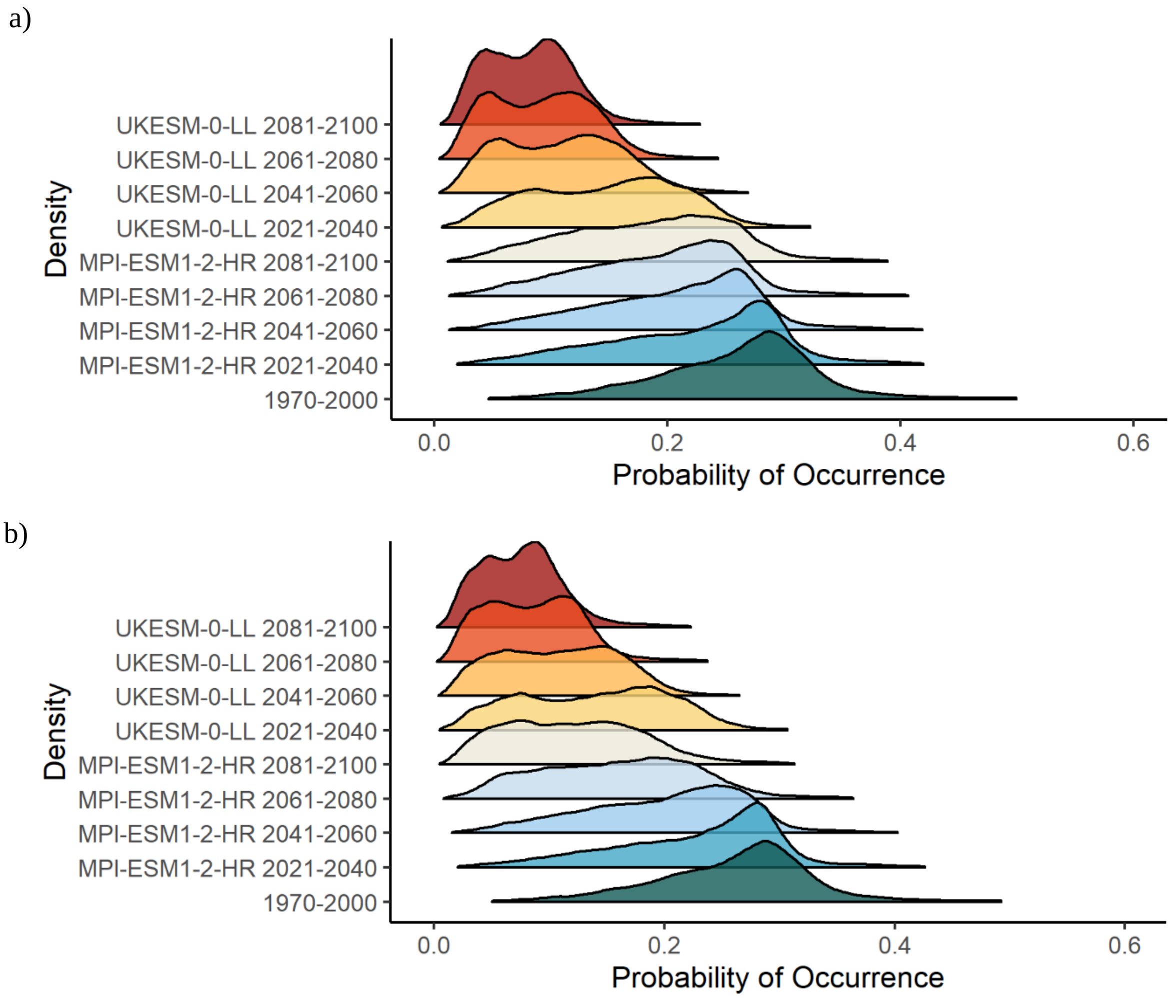

Figure 1.4 Densities of probability of occurrence of *J. ashei* within the breeding range of *S. chrysoparia* over the next century using two generalized circulation models under a) SSP2-4.5 (middle-of-the-road) and b) SSP3-7.0 (regional rivalry). Plots were built using a sample of the entire dataset (n = 1,018,552)

Projected Impacts on *S. chrysoparia* Distribution

Based on the historical *J. ashei* conditions, *S. chrysoparia* habitat adds up to 1,119.9 km^2 of optimal habitat and 9,729 km^2 of marginal habitat totaling to 10,848.9 km^2 of the most suitable habitat (Figure 1.5 and 1.6). The majority of the optimal and marginal habitat is distributed in the southern and southeastern regions of the *S. chrysoparia* breeding range, with some fragmented areas of marginal habitat existing in the northern part of the range (Figure 1.5).

Under the future climate scenarios, the projected reductions in the suitable conditions of *J. ashei* are likely to lead to large losses of suitable habitat for *S. chrysoparia*. Under the SSP2-4.5 scenario, the MPI-ESM1-2-HR model projects habitat to remain relatively stable in the first period (2021-2040), but by the 2081-2100 period, this model projects a reduction of optimal and marginal habitat to 1,081 km^2 and 8,149 km^2, respectively (total loss of 14.9%) (Figure 1.6). For the projection from this same GCM using the SSP3-7.0 scenario, a slight increase in optimal habitat is predicted (0.195%) in the first time period (2021-2040), but the expanse of optimal and marginal habitat gradually reduces to as little as 613.8 km^2 and 2,799.4 km^2, respectively (total loss of 69%) (Figure 1.6). The areas of marginal and optimal habitat that remain by the end of the century are distributed along the central region of the breeding range, near the City of Austin and the military installation, Fort Cavazos (Figure 1.5).

Under the hotter and wetter climate scenario (UKESM1-0-LL), both SSP2-4.5 and SSP3-7.0 predict similar reductions in *S. chrysoparia* habitat across all time periods (Figure 1.5 and 1.6). By the first time period (2021-2040), this GCM predicts a drastic reduction of marginal and optimal habitat with approximately 5,000 km^2 and 800 km^2 left, respectively (at most 46% loss). For both SSPs, by the last time period (2081-2100), UKESM1-0-LL predicts that marginal and optimal habitat will drop to at least 185 km^2 and 93.4 km^2, respectively (at most 97% total loss) (Figure 1.5 and 1.6). UKESM1-0-LL does predict the most extreme loss of marginal and optimal *S. chrysoparia* habitat, reducing the distribution to only the areas surrounding Austin, Texas and the Fort Cavazos military installation in the east central region of the breeding range.

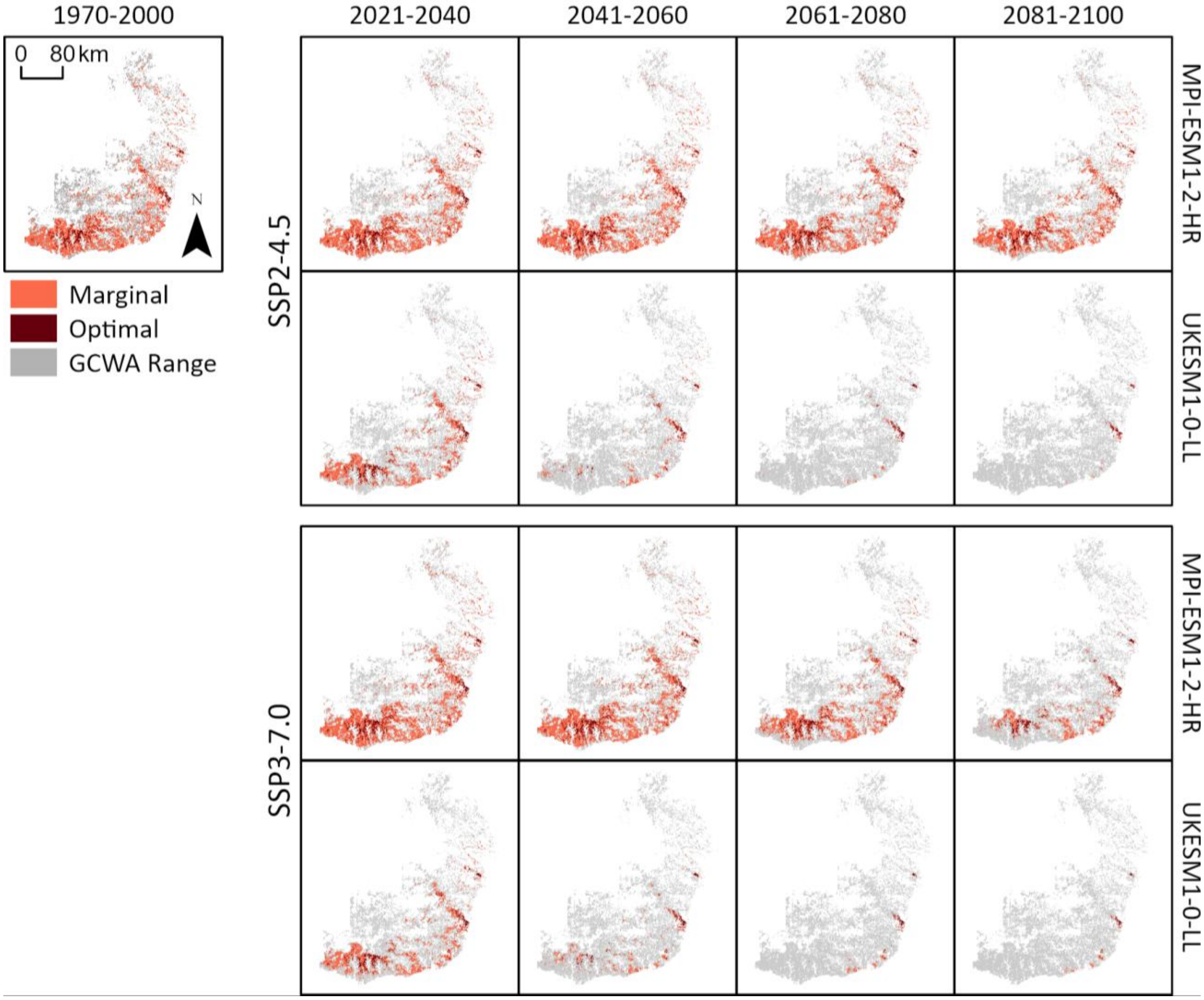

Figure 1.5 Distributional change of marginal and optimal *S. chrysoparia* habitat under two climate models under SSP2-4.5 (middle-of-the-road) and SSP3-7.0 (regional rivalry) by 2100. Using a density model by Mueller et al. (2022), densities between 0.0625-0.25 males/ha are considered marginal habitat and densities ≥0.25 males/ha are considered optimal habitat. Under the hottest and wettest conditions in the regional rivalry emissions scenario (UKESM1 SSP3-7.0), the remaining areas of potentially suitable *S. chrysoparia* habitat are in the southeastern edge of the range.

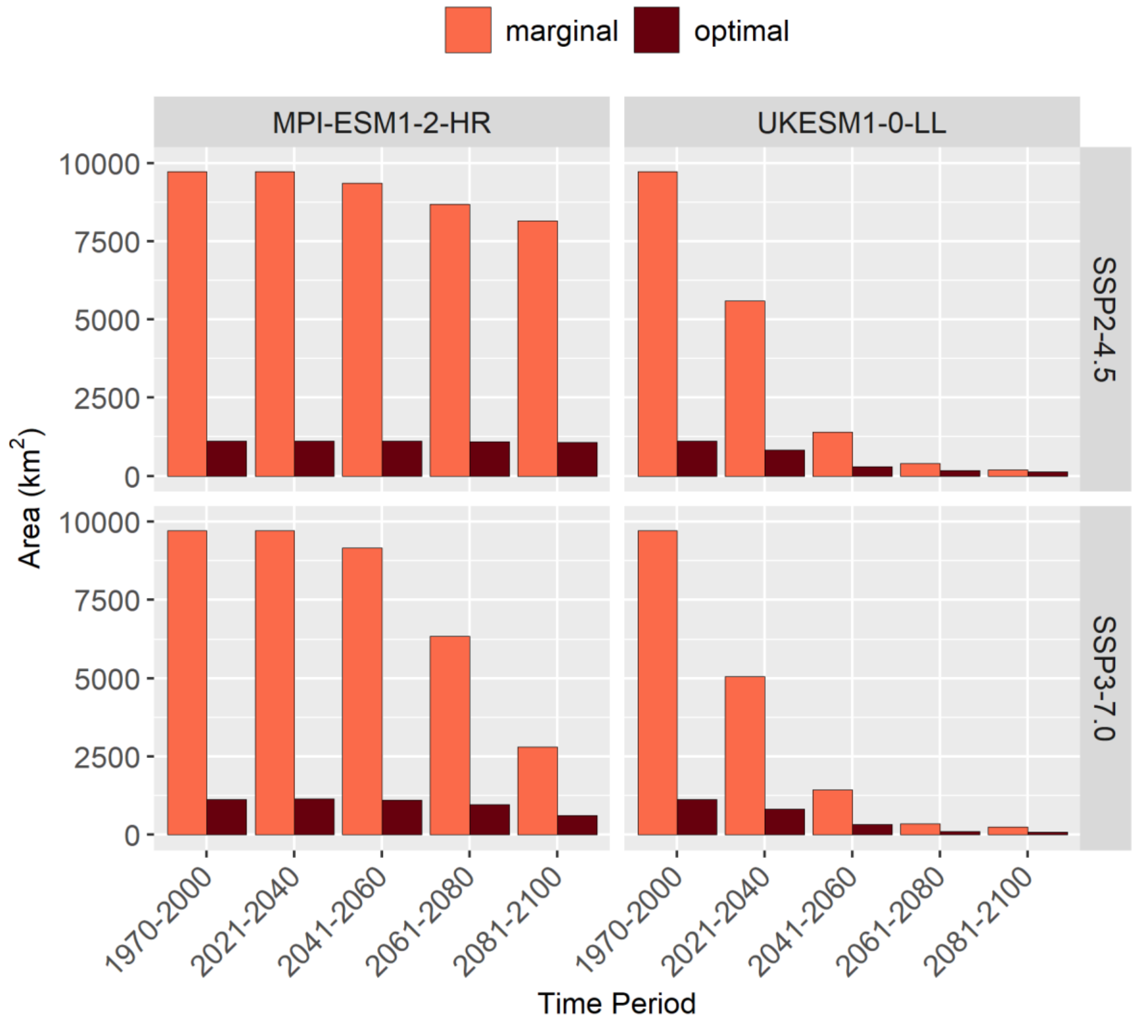

Figure 1.6 Amount of potential warbler habitat loss under three climate models by 2100 under SSP2-4.5 (middle-of-the-road) and SSP3-7.0 (regional rivalry). Historic (1970-2000) expanse of marginal and optimal warbler habitat is included in every plot for reference. Under the hottest and wettest conditions in the regional rivalry emissions scenario (UKESM1-0-LL), we may see a loss of nearly 9,484.6 km^2 of marginal habitat and 1,026.5 km^2 of optimal habitat.

DISCUSSION

At-risk species often face multiple threats causing them to have greatly reduced population numbers. Climate change has the potential to push many of these species over the edge. Determining the impact of climate change on *J. ashei*, a non-resprouting tree species, is crucial to assessing the future of *S. chrysoparia* habitat due to its importance to nest construction (Ladd and Gass 1999). Our results indicate that climate change is likely to reduce the suitability of the region for *J. ashei* resulting in a contraction of the distribution of *S. chrysoparia* habitat.

Conservation management of species has increasingly focused on mitigating the impacts of climate change, especially for at-risk species (Wilkening et al. 2019, Bateman et al. 2020). By leveraging a range of climate models for projecting species distributions, managers can assess the feasibility of conservation strategies and determine priorities. The GCMs we used for our study offer two different projected climatic futures with MPI-ESM1-2-HR representing a low to moderate increase and UKESM1-0-LL representing a major increase in the annual means of both temperature and precipitation. Under MPI-ESM1-2-HR scenarios, although they still predict contraction in both *J. ashei* and *S. chrysoparia* distributions, management actions could still be implemented to reduce the potential impacts of climate change. On the other hand, the UKESM1-0-LL scenarios pose a real threat to the persistence of both *J. ashei* and *S. chrysoparia*.

According to our model validation, the ensembled model showed good performance and predicted historical conditions similarly to previous *J. ashei* distribution and abundance models (Gray et al. 2012). The threshold-based distribution accurately predicted occurrence in all three major ecoregions of Texas (Edwards Plateau, Cross-Timbers, and Post Oak Savannah) in which *J. ashei* occurs in larger numbers and in diverse community structures (Griffith et al. 2007). Our approach, which integrated both regression-based and machine learning-based algorithms under standard parameters, worked efficiently and accurately to predict the historical distribution.

Likewise, the most important variables in our model are well aligned with species biology. Based on our individual models and the weighted ensemble model, the most important variables driving *J. ashei* distribution included precipitation of warmest quarter (bio18), mean diurnal temperature range (bio2), and available water storage at the root zone. Because available water storage was incorporated as a static variable, precipitation of the warmest quarter and mean diurnal temperature range were the variables that played the most significant role in determining *J. ashei* suitability. The decreased average precipitation of warmest quarter in the more extreme models could likely be driving the decrease in *J. ashei* suitability impacting the persistence of *S. chrysoparia* habitat. Our modeling results showed that under increased temperatures and decreased summer rainfall as predicted by the UKESM1-0-LL GCM, we may observe an extensive reduction in suitability for *J. ashei*. Within the breeding range of *S. chrysoparia*, the *J. ashei* distribution contraction ranged between 70% (MPI-ESM1-2-HR SSP2-4.5) and 99% (UKESM1-0-LL SSP2-4.5 and SSP3-7.0) by 2100.

Our projections of potential distribution contraction are comparable to the species distribution models of two *Juniperus* species in northern Mexico, *J. jaliscana* and *J. monticola*, which saw projected reductions between 55% to 93% (Pérez-Suárez et al. 2024). Unfortunately, the level of reduction of the most suitable habitat for *S. chrysoparia* due to resource loss could be so drastic that the remaining area may not be able to sustain a healthy population. The UKESM1-0-LL projections resulted in a widespread loss of optimal and marginal habitat for *S. chrysoparia*—approximately 10,511 km^2 of habitat loss (-97%) by 2100. Even under the less extreme climate scenarios (MPI-ESM1-2-HR), *S. chrysoparia* habitat is still predicted to decrease by at least 14.9% by 2100.

When we applied our model to a much larger spatial extent than presented here, some models projected an increase in suitability in north central United States. However, the possibility of *J. ashei* or *S. chrysoparia* dispersing northward past the vast agricultural lands of the states north of Texas to follow the bioclimatic niche is likely quite low. Additionally, if available water storage had been incorporated as a dynamic predictor influenced by climatic changes, the distributional reduction of *J. ashei* could likely be even more pronounced.

Although our SDM doesn't incorporate the potential increase in water use efficiency driven by the increased CO_2 concentrations, which could allow junipers to persist in drier regions, previous research has shown that drought and extreme heat pose an immense threat to the resilience of *J. ashei* and associated communities (Mathias and Thomas 2021). In the Edwards Plateau, for example, Schwantes et al. (2017) noted that the historical mean annual precipitation was about 614 mm, whereas during the 2011 drought, the average precipitation reduced to 295 mm. Although *J. ashei* had been thought to be a drought-tolerant species, recent research has shown mass mortality events and increased dynamic water stress following drought, which means that extreme drought events could further reduce our projected distributions (Polley et al. 2018, Schwantes et al. 2018). Likewise, less suitable conditions have been found to increase vulnerability to drought, further amplifying the impact of climate change if suitable conditions worsen within the next century (Johnson et al. 2018).

Climate change is not only impacting long-term climate means and severe droughts, but it is also leading to increased severity and frequency of wildfires (Bailey & van de Pol 2016, Maxwell et al. 2019). Pre-settlement, old-growth juniper-oak woodlands most likely experienced long fire-free intervals thus maintaining the mature juniper necessary for *S. chrysoparia* breeding habitat. However, research has found that *S. chrysoparia* prefer to use mature woodlands that have experienced low intensity surface fires that open up the understory, showing the importance of fire in this ecosystem (Reidy et al. 2021). Before this region became increasingly developed, Indigenous peoples and native browsing mammals helped maintain the mosaic of savannas, shrublands and woodlands that *J. ashei* is associated with through the intentional use of fire, which reduced fuel loads and kept surface fires from developing into crown fires (Fowler and Carden 2024, Stambaugh et al. 2014, Stambaugh et al. 2017). By contrast, the larger and more severe fires likely to come with climate change will possibly result in fewer older trees on the landscape.

Although we focused our modeling on *J. ashei*, *Quercus spp.* also serve a significant part in *S. chrysoparia* habitat suitability. The dynamic roles of *Quercus spp.* and *J. ashei* in perching, territoriality and foraging behaviors as the breeding season progresses shows the importance of also determining the impact of climate change on oak species (Long et al. 2021). Assessing the potential changes in warbler habitat suitability will require an understanding of how these bioclimatic shifts will impact not only these important resources but also the successional dynamics and structure of this landscape in this increasingly urbanized region. Since the 1800s, juniper-oak woodlands have been encroaching on grassland and savanna ecosystems due to the removal and genocide of Indigenous peoples, the rise of fire suppression, and the increase in deer herbivory (Fowler and Carden 2024, Stambaugh et al. 2014, Stambaugh et al. 2017). The deciduous communities show low recruitment due to deer herbivory with research showing an abundance of juvenile trees, but only a few saplings and mature trees for both oaks and junipers (Van Auken et al. 2023, Andruk et al. 2014). Under extreme climatic conditions and increasing herbivore disturbance, the size distribution and structure of these woodlands will continue to change. Increasing fuel loads and oak-recruitment failure have even led to “juniperization” in some regions, creating what are close to *J. ashei* monocultures that no longer provide optimal *S. chrysoparia* habitat. Although mechanical removal and prescribed fire management treatments have been implemented with the goals of reducing fuel loads and promoting oak regeneration, the fire regime and successional dynamics of central Texas communities have been largely impacted making it increasingly more prone to extreme fire and drought events that can result in mass mortality (Reidy et al. 2021, Fowler and Carden 2024, Gao et al. 2021, Nielson-Gammon et al. 2020). Our study explored the effects of climate-induced resource loss through a species distribution modeling approach, but further mechanistic research should be conducted to assess the potential additive or synergistic effects these added stressors will have on the habitat distributions of *J. ashei* and *S. chrysoparia*.

Our study demonstrates how *S. chrysoparia* dependence on *J. ashei* will likely limit the species’ capacity to adapt to this changing landscape. Recent research has found similar predictions of reduced population viability for *S. chrysoparia* but through the lens of increased severity and frequency of extreme climate events like El Niño events (Reidy et al. 2023). Although *S. chrysoparia* population estimates have been larger in recent years in comparison to the original estimate during the USFWS 1990 listing, urbanization and climate change are expected to continue to impact habitat suitability throughout its breeding range (Mueller et al. 2022, Mathewson et al. 2012). The outcome of our study allows us to determine regions in which *J. ashei* will likely struggle to persist and regenerate under a changing climate, bearing substantial conservation implications for this endangered songbird. Along with climate change mitigation strategies, to conserve warbler populations, managers will want to focus on protecting and restoring *J. ashei* and its associated communities within areas of the Edwards Plateau where it is most likely to remain as the climate changes.

Supplementary material

Supplementary material is available at *Ornithology/Ornithological Applications* online.

Acknowledgements

We thank F. Crossway, L. Wahl, and B. Harvey for providing extensive insight into project development and manuscript feedback.

Funding statement. *(required and must include grant numbers)*

This work is supported by the Strategic Environmental Research and Development Program (SERDP) (grant no. RC22-3437) from the Department of Defense. Additional funding was provided by the School of Environmental and Forest Sciences' Bridging the Gap Fellowship, Dorothie and Ernest Knoblauch Endowed Fellowship, Agnes Healy Anderson Forestry Graduate Research Fellowship, Byron and Alice Lockwood Endowed Fellowship Fund, and James Ridgeway Endowed Scholarship

Ethics statement.

We did not conduct field or lab work.

Author contributions.

L.S.F. and J.J.L. conceived the idea of the study. J.J.L. and J.A.H. obtained funding. L.S.F. processed the data and built the model. J.J.L assisted in modelling. L.S.F wrote the first draft of the manuscript. All authors provided input, reviewed, and edited manuscript.

Data availability.

LITERATURE CITED

Ahmad, R., A. A. Khuroo, B. Charles, M. Hamid, I. Rashid, and N. A. Aravind. 2019. Global distribution modelling, invasion risk assessment and niche dynamics of Leucanthemum vulgare (Ox-eye Daisy) under climate change. Scientific Reports 9:11395.

Aiello-Lammens, M. E., R. A. Boria, A. Radosavljevic, B. Vilela, and R. P. Anderson. 2015. spThin: an R package for spatial thinning of species occurrence records for use in ecological niche models. Ecography 38:541–545.

Andruk, C. M., C. Schwope, and N. L. Fowler. 2014. The joint effects of fire and herbivory on hardwood regeneration in central Texas woodlands. Forest Ecology and Management 334:193–200.

Babak Naimi. 2023, 29. usdm: Uncertainty Analysis for Species Distribution Models.

Bailey, L. D., and M. van de Pol. 2016. Tackling extremes: challenges for ecological and evolutionary research on extreme climatic events. Journal of Animal Ecology 85:85–96.

Barbet-Massin, M., F. Jiguet, C. H. Albert, and W. Thuiller. 2012. Selecting pseudo-absences for species distribution models: how, where and how many? Methods in Ecology and Evolution 3:327–338.

Bateman, B. L., C. Wilsey, L. Taylor, J. Wu, G. S. LeBaron, and G. Langham. 2020. North American birds require mitigation and adaptation to reduce vulnerability to climate change. Conservation Science and Practice 2:e242.

Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. Ecological Modelling 157:281–300.

Chamberlain S, Barve V, Mcglinn D, Oldoni D, Desmet P, Geffert L, Ram K (2024). *rgbif: Interface to the Global Biodiversity Information Facility API*. R package version 3.8.1, https://CRAN.R-project.org/package=rgbif.

Crouchet, S. E., J. Jensen, B. F. Schwartz, and S. Schwinning. 2019. Tree Mortality After a Hot Drought: Distinguishing Density-Dependent and -Independent Drivers and Why It Matters. Frontiers in Forests and Global Change 2.

Di Cola, V., O. Broennimann, B. Petitpierre, F. T. Breiner, M. D'Amen, C. Randin, R. Engler, J. Pottier, D. Pio, A. Dubuis, L. Pellissier, R. G. Mateo, W. Hordijk, N. Salamin, and A. Guisan. 2017. ecospat: an R package to support spatial analyses and modeling of species niches and distributions. Ecography 40:774–787.

Diamond, D. D. 1997. An Old-Growth Definition for Western Juniper Woodlands: Texas Ashe Juniper Dominated or Codominated Communities. Gen. Tech. Rep. SRS-15. U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC.

Fick, S.E. and R.J. Hijmans, 2017. WorldClim 2: new 1km spatial resolution climate surfaces for global land areas. International Journal of Climatology 37 (12): 4302-4315.

Fowler, N. L., and R. E. Carden. 2024. Roles of fire in the plant communities of the eastern Edwards Plateau of Texas. Fire Ecology 20:55.

Fuhlendorf, S. D., F. E. Smeins, and W. E. Grant. 1996. Simulation of a fire-sensitive ecological threshold: a case study of Ashe juniper on the Edwards Plateau of Texas, USA. Ecological Modelling 90:245–255.

Gao, P., A. J. Terando, J. A. Kupfer, J. Morgan Varner, M. C. Stambaugh, T. L. Lei, and J. Kevin Hiers. 2021. Robust projections of future fire probability for the conterminous United States. Science of The Total Environment 789:147872.

GBIF.org (13 March 2024) GBIF Occurrence Download https://doi.org/10.15468/dl.x7dega

Gray, A. N.; T. J. Brandeis, J. D. Shaw, W. H. McWilliams, P. D. Miles. 2012. Forest Inventory and Analysis Database of the United States of America (FIA). In: Dengler, J.; Oldeland, J.; Jansen, F.; Chytry, M.; Ewald, J., Finckh, M.; Glockler, F.; Lopez-Gonzalez, G.; Peet, R. K.; Schaminee, J .H. J., eds. Vegetation databases for the 21st century. Biodiversity and Ecology. 4: 225-231.

Griffith, G., S. Bryce, J. Omernik, and A. Rogers. 2007. Ecoregions of Texas. Texas Commission on Environmental Quality, pp. 134.

Gutjahr, O., D. Putrasahan, K. Lohmann, J. H. Jungclaus, J.-S. von Storch, N. Brüggemann, H. Haak, and A. Stössel. 2019. Max Planck Institute Earth System Model (MPI-ESM1.2) for the High-Resolution Model Intercomparison Project (HighResMIP). Geoscientific Model Development 12:3241–3281.

Hargrove, W. W. 2016. Home Range Shifts for Juniperus ashei Predicted Under Climatic Change.

Hijmans R (2025). *terra: Spatial Data Analysis*. R package version 1.8-30, https://github.com/rspatial/terra.

Hijmans, R. J. 2012. Cross-validation of species distribution models: removing spatial sorting bias and calibration with a null model. Ecology 93:679–688.

Hirzel, A. H., G. Le Lay, V. Helfer, C. Randin, and A. Guisan. 2006. Evaluating the ability of habitat suitability models to predict species presences. Ecological Modelling 199:142–152.

Hitch, A. T., and P. L. Leberg. 2007. Breeding Distributions of North American Bird Species Moving North as a Result of Climate Change. Conservation Biology 21:534–539.

Johnsen, T.N. and Alexander, R.A., 1974. Juniperus L. In: C.S. Schopmeyer (Technical Coord.), Seeds of Woody Plants in the United States. Agric. Handbook 450, USDA Forest Serv., pp. 460-469.

Johnson, D. M., J.-C. Domec, Z. Carter Berry, A. M. Schwantes, K. A. McCulloh, D. R. Woodruff, H. Wayne Polley, R. Wortemann, J. J. Swenson, D. Scott Mackay, N. G. McDowell, and R. B. Jackson. 2018. Co-occurring woody species have diverse hydraulic strategies and mortality rates during an extreme drought. Plant, Cell & Environment 41:576–588.

Kopecký, M., M. Macek, and J. Wild. 2021. Topographic Wetness Index calculation guidelines based on measured soil moisture and plant species composition. Science of The Total Environment 757:143785.

Ladd, C., and L. Gass. 1999. Golden-cheeked Warbler (Setophaga chrysoparia), version 1.0. Birds of the World.

Long, A. M., H. A. Mathewson, and M. L. Morrison. 2021. The influence of geographic variation in vegetation characteristics on habitat use and productivity of an endangered warbler. Forest Ecology and Management 482:118857.

Mathewson, H. A., J. E. Groce, T. M. McFarland, M. L. Morrison, J. C. Newnam, R. T. Snelgrove, B. A. Collier, and R. N. Wilkins. 2012. Estimating breeding season abundance of golden-cheeked warblers in Texas, USA. The Journal of Wildlife Management 76:1117–1128.

Mathias, J. M., and R. B. Thomas. 2021. Global tree intrinsic water use efficiency is enhanced by increased atmospheric CO2 and modulated by climate and plant functional types. Proceedings of the National Academy of Sciences 118:e2014286118.

Maxwell, S. L., N. Butt, M. Maron, C. A. McAlpine, S. Chapman, A. Ullmann, D. B. Segan, and J. E. M. Watson. 2019. Conservation implications of ecological responses to extreme weather and climate events. Diversity and Distributions 25:613–625.

Mueller, J. M., S. E. Sesnie, S. E. Lehnen, H. T. Davis, J. J. Giocomo, J. N. Macey, and A. M. Long. 2022. Multi-scale species density model for conserving an endangered songbird. The Journal of Wildlife Management 86:e22236.

Naimi, B., and M. B. Araújo. 2016. sdm: a reproducible and extensible R platform for species distribution modelling. Ecography 39:368–375.

Nielsen-Gammon, J., S. Holman, A. Buley, S. Jorgensen, J. Escobedo, C. Ott, J. Dedrick, and Van Fleet, Ali. 2021. Assessment of Historic and Future Trends of Extreme Weather in Texas, 1900-2036: 2021 Update. Office of the State Climatologist, Texas A&M University, College Station:44.

O'Brien, J. 2020. rasterDT: *Fast Raster Summary and Manipulation*. R package version 0.3.2, https://cran.r-project.org/web/packages/rasterDT. Accessed 20 Feb. 2024.

O’Neill, B. C., C. Tebaldi, D. P. van Vuuren, V. Eyring, P. Friedlingstein, G. Hurtt, R. Knutti, E. Kriegler, J.-F. Lamarque, J. Lowe, G. A. Meehl, R. Moss, K. Riahi, and B. M. Sanderson. 2016. The Scenario Model Intercomparison Project (ScenarioMIP) for CMIP6. Geoscientific Model Development 9:3461–3482.

Parding, K. M., A. Dobler, C. F. McSweeney, O. A. Landgren, R. Benestad, H. B. Erlandsen, A. Mezghani, H. Gregow, O. Räty, E. Viktor, J. El Zohbi, O. B. Christensen, and H. Loukos. 2020. GCMeval – An interactive tool for evaluation and selection of climate model ensembles. Climate Services 18:100167.

Pérez-Suárez, M., J. E. Ramírez-Albores, and Á. R. Martínez-Campos. 2024. Predicting the impacts of climate change on potential suitability habitats of three Juniperus trees in Mexico. Plant Ecology 225:37–51.

Peters, M. P., L. R. Iverson, A. M. Prasad, and S. N. Matthews. 2013. Integrating fine-scale soil data into species distribution models: preparing Soil Survey Geographic (SSURGO) data from multiple counties. Page NRS-GTR-122. U.S. Department of Agriculture, Forest Service, Northern Research Station, Newtown Square, PA.

Polley, H. W., D. M. Johnson, and R. B. Jackson. 2016. Canopy foliation and area as predictors of mortality risk from episodic drought for individual trees of Ashe juniper. Plant Ecology 217:1105–1114.

Polley, H. W., D. M. Johnson, and R. B. Jackson. 2018. Projected drought effects on the demography of Ashe juniper populations inferred from remote measurements of tree canopies. Plant Ecology 219:1259–1267.

Portalier, S. M. J., J.-N. Candau, and F. Lutscher. 2022. A temperature-driven model of phenological mismatch provides insights into the potential impacts of climate change on consumer–resource interactions. Ecography 2022:e06259.

Pulich, W. M. 1976. Review of The Golden-Cheeked Warbler. The Auk 94:799–801.

R Core Team (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Reemts, C. M., and L. L. Hansen. 2008. Slow recolonization of burned oak–juniper woodlands by Ashe juniper (Juniperus ashei): Ten years of succession after crown fire. Forest Ecology and Management 255:1057–1066.

Reemts, C. M., C. Picinich, and J. H. Sperry. 2024. Crown fires remove a fire-sensitive canopy dominant from oak-juniper woodlands: results from long-term monitoring of wildfires. Fire Ecology 20:73.

Reidy, J. L., E. A. Sinnott, F. R. Thompson III, and L. O'Donnell. 2023. Urban land cover and El Niño events negatively impact population viability of an endangered North American songbird. Ecosphere 14:e4583.

Reidy, J. L., F. R. Thompson, S. Rowin, C. Schwope, and J. M. Mueller. 2021. Effects of prescribed fire on fuels, vegetation, and Golden-cheeked warbler (*Setophaga chrysoparia*) demographics in Texas juniper-oak woodlands: An update six years post-fire. Forest Ecology and Management 492:119191.

Schwantes, A. M., A. J. Parolari, J. J. Swenson, D. M. Johnson, J.-C. Domec, R. B. Jackson, N. Pelak, and A. Porporato. 2018. Accounting for landscape heterogeneity improves spatial predictions of tree vulnerability to drought. New Phytologist 220:132–146.

Schwantes, A. M., J. J. Swenson, M. González-Roglich, D. M. Johnson, J.-C. Domec, and R. B. Jackson. 2017. Measuring canopy loss and climatic thresholds from an extreme drought along a fivefold precipitation gradient across Texas. Global Change Biology 23:5120–5135.

Schwantes, A., J. Swenson, and R. Jackson. 2016. Quantifying drought-induced tree mortality in the open canopy woodlands of central Texas. Remote Sensing of Environment 181:54–64.

Sellar, A. A., C. G. Jones, J. P. Mulcahy, Y. Tang, A. Yool, A. Wiltshire, F. M. O'Connor, M. Stringer, R. Hill, J. Palmieri, S. Woodward, L. de Mora, T. Kuhlbrodt, S. T. Rumbold, D. I. Kelley, R. Ellis, C. E. Johnson, J. Walton, N. L. Abraham, M. B. Andrews, T. Andrews, A. T. Archibald, S. Berthou, E. Burke, E. Blockley, K. Carslaw, M. Dalvi, J. Edwards, G. A. Folberth, N. Gedney, P. T. Griffiths, A. B. Harper, M. A. Hendry, A. J. Hewitt, B. Johnson, A. Jones, C. D. Jones, J. Keeble, S. Liddicoat, O. Morgenstern, R. J. Parker, V. Predoi, E. Robertson, A. Siahaan, R. S. Smith, R. Swaminathan, M. T. Woodhouse, G. Zeng, and M. Zerroukat. 2019.

UKESM1: Description and Evaluation of the U.K. Earth System Model. Journal of Advances in Modeling Earth Systems 11:4513–4558.

Soil Survey Staff. Gridded Soil Survey Geographic (gSSURGO) Database for the Conterminous United States. United States Department of Agriculture, Natural Resources Conservation Service. Available online at https://gdg.sc.egov.usda.gov/. *January 1, 2024* (202007 official release).

Stambaugh, M. C., G. Creacy, J. Sparks, and M. Rooney. 2017. Three centuries of fire and forest vegetation transitions preceding Texas' most destructive wildfire: Lost Pines or lost oaks? Forest Ecology and Management 396:91–101.

Stambaugh, M. C., J. C. Sparks, and E. R. Abadir. 2014. Historical Pyrogeography of Texas, USA. Fire Ecology 10:72–89.

Twining, C. W., J. R. Shipley, and B. Matthews. 2022. Climate change creates nutritional phenological mismatches. Trends in Ecology & Evolution 37:736–739.

Urban, M. C. 2015. Accelerating extinction risk from climate change. Science 348:571–573.

U.S. Fish and Wildlife Service [USFWS]. 1990a. Endangered and threatened wildlife and plants—emergency rule to list the golden-cheeked warbler as endangered. Federal Register 55:18844–18845

U.S. Geological Survey, 2019, 3D Elevation Program 1 arc-second Resolution Digital Elevation Model (published 20200606), accessed January 18, 2024 at URL https://www.usgs.gov/the-national-map-data-delivery

Van Auken, O. W., J. K. Bush, D. L. Taylor, and J. R. Singhurst. 2023. Lack of woody species recruitment in isolated deep canyon deciduous woodlands in central Texas, USA1. The Journal of the Torrey Botanical Society 150:525–537.

Wahl, R., D. D. Diamond, and D. Shaw. 1990. The golden-cheeked warbler: a status review. Austin, Texas, USA.

Wilkening, J., W. Pearson-Prestera, N. A. Mungi, and S. Bhattacharyya. 2019. Endangered species management and climate change: When habitat conservation becomes a moving target. Wildlife Society Bulletin 43:11–20.

Yukimoto, S., H. Kawai, T. Koshiro, N. Oshima, K. Yoshida, S. Urakawa, H. Tsujino, M. Deushi, T. Tanaka, M. Hosaka, S. Yabu, H. Yoshimura, E. Shindo, R. Mizuta, A. Obata, Y. Adachi, and M. Ishii. 2019. The Meteorological Research Institute Earth System Model Version 2.0, MRI-ESM2.0: Description and Basic Evaluation of the Physical Component. Journal of the Meteorological Society of Japan. Ser. II 97:931–965.

CHAPTER 2.

Projected population responses of the endangered Golden-cheeked Warbler (*Setophaga chrysoparia*) to climate change-induced habitat loss.

Leticia Santillana Fernandez[1*], Sydney Watkins[2], Julie A. Heinrichs[2], Elizabeth Law[2], Marc Pons[2], Shelley Nelson[2], Fern Crossway[1], Joshua J. Lawler[1]
[1]School of Environmental and Forest Sciences, University of Washington, Seattle, Washington, USA
[2] Computational Ecology Group Inc., Canmore, Alberta, Canada
*Corresponding author: letysf18@uw.edu

Keywords: Golden-cheeked Warbler, Ashe juniper, climate change, population dynamics, simulation, distribution, habitat, endangered species

Acknowledgements text (here)

We thank the Computation Ecology Group (CEG) and Nathan Schumaker for their invaluable assistance with model conceptualization and model building. This work is supported by the Strategic Environmental Research and Development Program (SERDP) (grant no. RC22-3437) from the Department of Defense. Additional funding was provided by the School of Environmental and Forest Sciences' Bridging the Gap Fellowship, Dorothie and Ernest Knoblauch Endowed Fellowship, Agnes Healy Anderson Forestry Graduate Research Fellowship, Byron and Alice Lockwood Endowed Fellowship Fund, and James Ridgeway Endowed Scholarship. We thank all of our collaborators who have provided data, ecosystem and species expertise including John Macey and Virginia Sanford at Fort Cavazos, and Jennifer L. Reidy at the University of Missouri.

Projected population responses of the endangered Golden-cheeked Warbler (*Setophaga chrysoparia*) to climate change-induced habitat loss.

ABSTRACT

Specialist species that depend on one or a few other specific species can be more vulnerable to climate change than generalists. The Golden-cheeked Warbler (*Setophaga chrysoparia*) is an endangered habitat specialist that requires mature Ashe junipers (*Juniperus ashei*) for nest construction. Recent drought-induced juniper mortality events indicate that climate change may have a significant impact on this critical component of warbler habitat, and in turn, on the warbler population. To project the potential implications of climate-induced habitat change on warbler abundance and distribution, we built a spatially explicit, individual-based, population model. We developed a baseline model as well as four alternative future climate projections for 2020-2090, from two generalized circulation models run for each of two shared socioeconomic pathways. By 2090, projections from the MPI-ESM1-2-HR model resulted in population declines of 10% and 51% for the SSP2-4.5 and SSP3-7.0 scenarios, respectively. Climate projections from the UKESM1-0-LL model resulted in population declines of 94% for both scenarios. In the UKESM1-0-LL SSP2-4.5 and SSP3-7.0 scenarios, a significant proportion—50% and 59%, respectively—of the persisting population occupied protected areas in 2090. We explored the potential for population persistence across 14 protected sites currently harboring Golden-cheeked Warbler populations. We found that only three were still occupied by warblers by 2090 under the most extreme scenarios. Our results suggest that climate-driven resource loss may lead to declines in Golden-cheeked Warbler populations under all climate scenarios. Nonetheless, our results indicate that there are likely to be some potential climatic refugia under even the most extreme scenarios that we explored. Refugia on lands that are not

currently protected could serve as new conservation opportunities whereas those on protected lands could focus management activities.

INTRODUCTION

For many species, climatic extremes and changing disturbance regimes can have lasting consequences on resource availability, habitat quality, and population densities. These factors have already led species to adapt to a changing climate by shifting their distributions and have regularly led to range contractions (Parmesan and Yohe 2003, Hitch & Leberg 2007, Bateman et al. 2020). Climate-mediated disruption of ecosystem processes, physiology, trophic networks and phenology have had cascading effects on species' adaptive capacity and dispersal ability (Roman-Palacios and Wiens 2020, Twinning et al. 2022, Bellard et al. 2012). The business-as-usual trajectory of a 4.3˚C increase predicts a global extinction risk of 16% (Urban 2015). Yet with climate mitigation strategies, a target of a 3˚C rise in global temperatures could reduce global extinction risk to 8.5%. However, exacerbated by increasing land-use change, climate change is predicted to not only increase species extinctions but accelerate them.

Climate change poses particularly large challenges for highly specialized species already at risk of extinction (Wilkening et al. 2019). The ability of such species to adapt to climate change will likely depend on how the species on which they rely will respond to climate change (Hitch and Leberg 2007, Both et al. 2009, Portalier et al. 2022). For example, the koala's dependence on specific *Eucalyptus* species for foraging has made the species highly vulnerable due to climate-induced shifts in the trees' distributions (Adams-Hosking et al. 2012). The populations of many species such as the ice-obligate polar bear or bamboo-obligate giant panda have been predicted to decline due to climate-induced resource loss (Li et al. 2015, Moore and Huntington 2008, Correll et al. 2019). Unfortunately, at-risk species face multiple, potentially interacting threats (e.g., habitat fragmentation, disease), which are likely to be compounded by climate change (Fontini and Dye 2017, Lawler et al. 2002).

The Golden-cheeked Warbler (*Setophaga chrysoparia*; warbler hereafter) is a habitat specialist that breeds exclusively in the Ashe juniper (*Juniperus ashei*)-oak (*Quercus spp.*) woodlands of central Texas (Pulich 1976). Recent studies define warbler habitat as being composed of 60-80% Ashe juniper canopy cover with relatively closed canopy and trees taller than 3 meters (Mueller et al. 2022). Taller, older Ashe junipers provide the warbler with a critical resource that make it a habitat specialist. Specifically, the warbler requires the shedding bark of older Ashe junipers for nest construction. In 1990, the warbler was listed as endangered under the Endangered Species Act due to extensive habitat loss and habitat fragmentation (USFWS 1990a). At that point, the population was estimated to be between 15,000-17,000 birds. With the vast majority of warbler habitat on private land, the small proportion of Texas that is designated as protected has been essential in conserving breeding habitat and enforcing management plans for the species (Ladd and Gass 1999; Dreiss et al. 2022; Duarte et al. 2013). These protected lands include parks, preserves, wildlife refuges, and military installations. However, its at-risk status and the fact that the warbler is so closely associated with Ashe juniper may make it particularly susceptible to climate change.

In the central United States and within Texas, studies have found that climate change will continue to increase the potential for high severity crown fires and drought-induced tree mortality (Reemts & Hansen 2008, Polley et al. 2018, Gao et al. 2021, Nielson-Gammon et al. 2021). These conditions will be worsened by high fuel loads that have resulted from historical fire suppression in this region. With increases in these extreme weather events, tree mortality of young and mature Ashe junipers will likely increase as has already been observed in the past decade (Johnson et al. 2018, Crouchet et al. 2019, Reemts et al. 2024, Reidy et al. 2021). For example, in 2011-2013, Texas endured a severe drought in which junipers experienced a mass mortality event with an approximate 27% canopy dieback within the Edwards Plateau (Polley et al. 2016, Johnson et al. 2018, Crouchet et al. 2019, Schwantes et al. 2016, 2017). Additionally, a recent model projected juniper mortality would increase through the 21st century due to an increase in dynamic water stress (Schwantes et al. 2018). Such climate effects on Ashe junipers will likely have cascading impacts on the Golden-cheeked Warbler.

Here, we explore how Golden-cheeked Warbler populations will likely respond to climate-driven resource loss. We built a spatially explicit, individual-based, population model using an existing warbler density model projection as a proxy for a habitat map (Mueller et al. 2022). We then simulated warbler populations under four climate-driven habitat change scenarios that incorporated projected shifts in the geographic distribution of Ashe juniper from 2020 to 2090. This approach allowed us to understand how both population size and spatial patterns of occupancy are likely to change in response to changes in the distribution of a key resource. We explicitly explored how the abundance of warblers in 14 protected areas that are currently managed for warbler persistence could change in the face of climatic impacts on Ashe juniper.

METHODS

General Approach

We built a spatially explicit, individual-based population model for the Golden-cheeked Warbler using the modeling framework HexSim (Version 4.0.20, Schumaker and Brookes 2018). HexSim allows the user to simulate unique individuals through a sequence of life history events (e.g., migration, reproduction, survival) through time and space. The modelling framework allows one to assign individuals traits, which can alter the way in which they interact with others or with the landscape. Series of spatial data layers can be used to simulate dynamic landscapes and different data layers can be used to influence different events in the model (e.g., movement, survival), which allows for landscape change over time or for simulated individuals to access multiple spatial layers depending on the life history event. These features facilitate the modeling of complex individual-based behaviors and dynamic spatial processes with the flexibility to incorporate various ecological processes (Lurgi et al. 2015).

We constructed a model that would provide a simple yet accurate representation of warbler behavior during the breeding season. The model included four basic life history events on an annual cycle: movement, territory selection, reproduction, and survival (Figure 2.1). All individuals in the model experienced each of the events before moving onto the next cycle (year). Because female warblers are cryptic and difficult to study, the demographic data available in the literature focus mainly on males. Therefore, we built a male-only model. Although the Golden-cheeked Warbler is a migratory species, we restricted the model to its breeding range to specifically focus on the impact of breeding habitat changes on male warblers (Figure 2.2). The spatial extent covered by the model was approximately 67,000 km^2, covering portions of the Edwards Plateau and Cross Timbers ecoregions of central Texas (Mueller et al. 2022). To simulate the population responses to climate-driven habitat change, we used modeled habitat loss resulting from projected climate-driven shifts in the distribution of Ashe juniper (Santillana Fernandez et al. *In prep*).

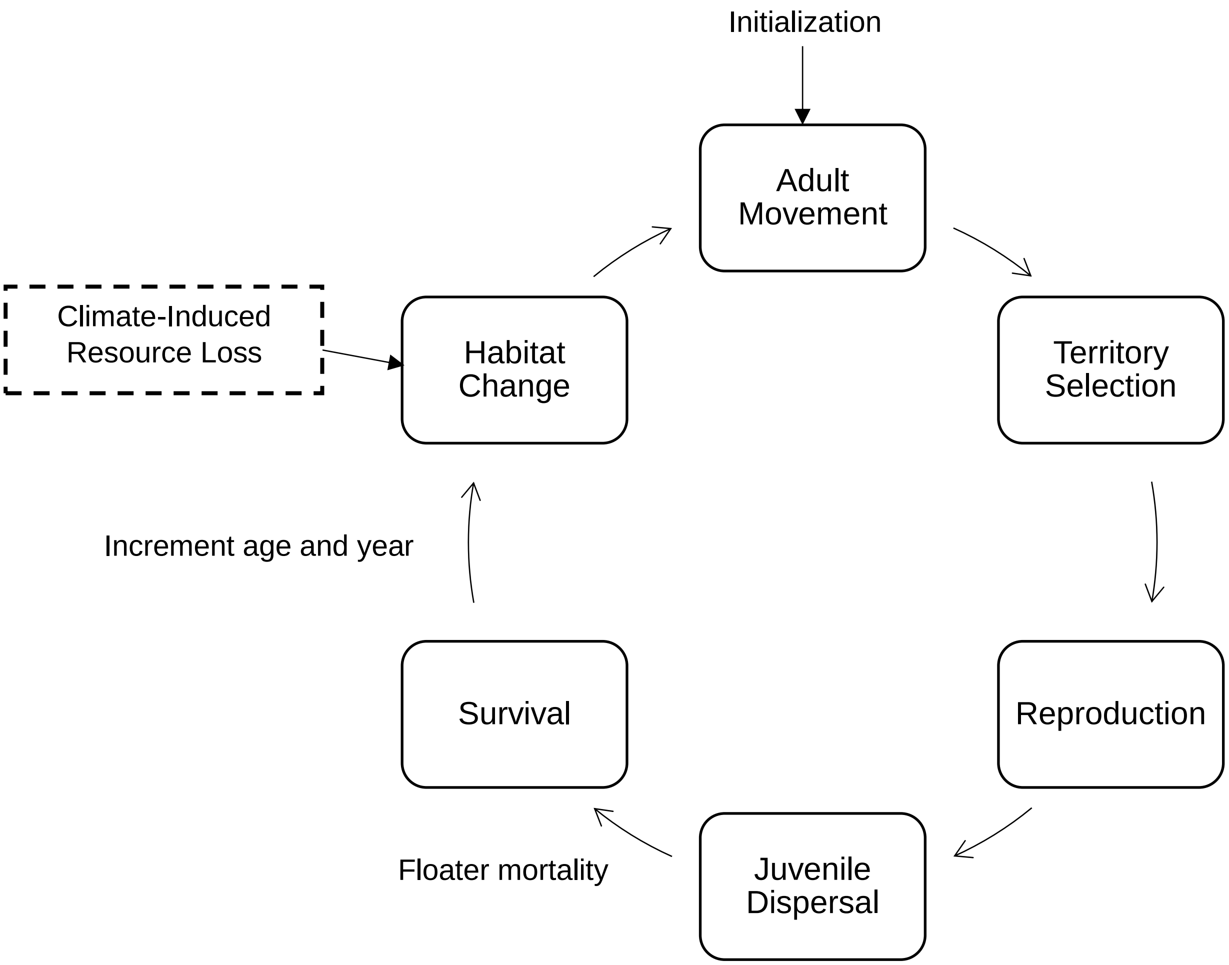

Figure 2.1 Simulated annual life cycle of the Golden-cheeked Warbler (*Setophaga chrysoparia*) responding to resource-loss induced habitat contraction.

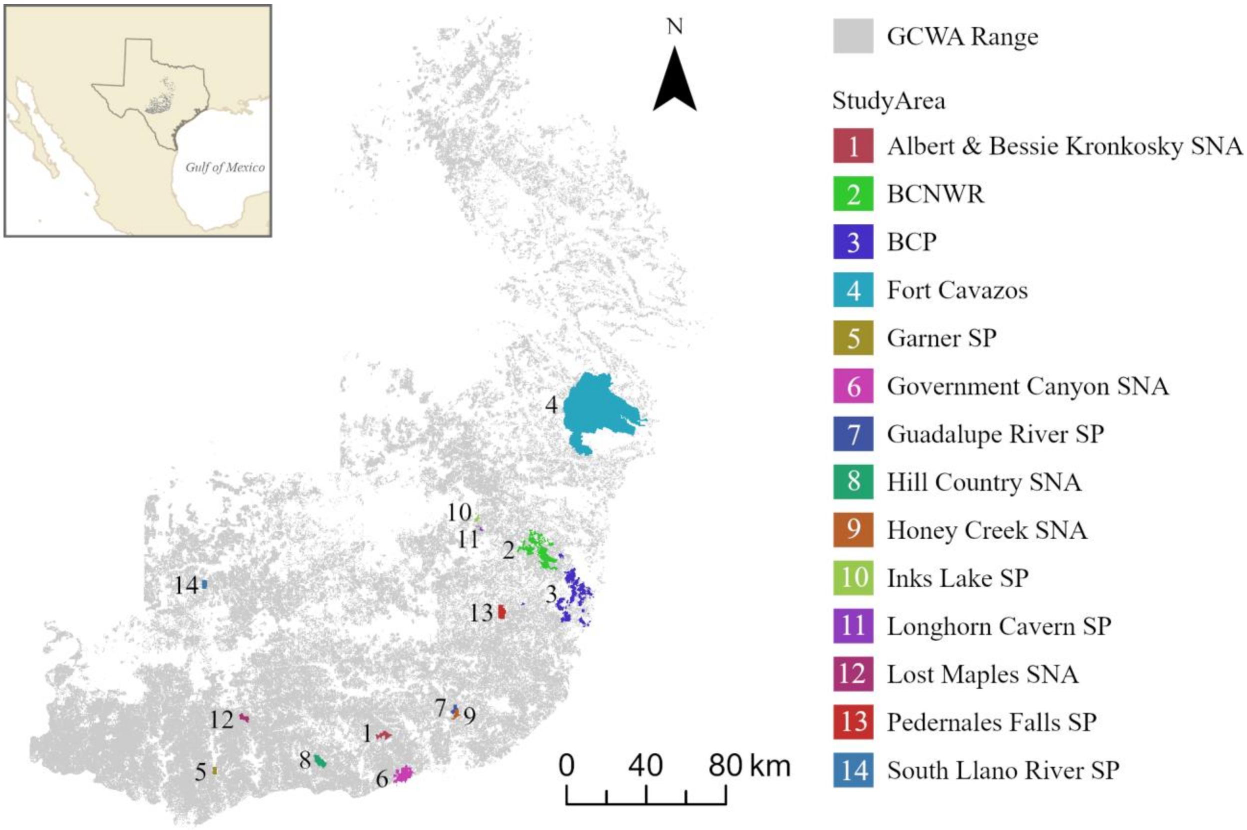

Figure 2.2 Breeding range of the Golden-cheeked Warbler (*Setophaga chrysoparia*) based on a density model by Mueller et al. (2022). The map shows several areas where Golden-cheeked Warbler habitat is protected or actively monitored within central Texas.

Historical Habitat Layer

Golden-cheeked Warbler demographics are strongly associated with habitat quality and site characteristics. Previous research has found that warbler densities >0.25 males/ha are found in the most optimal habitat, which is associated with 60-80% Ashe juniper cover (Mueller et al. 2022, Magness et al. 2006, Sesnie et al. 2016). A recent study found that this species does not pair successfully at low densities (< 0.02 males/ha), suggesting that density can be an appropriate metric to parameterize warbler demographics in our model (Farrell et al. 2012). Therefore, we used the density model by Mueller et al. (2022), which estimates the number of male warblers per hectare based on associated environmental predictors, as a projection of habitat quality. The density map was originally downloaded at a 10-m resolution but was resampled using bilinear interpolation to 100-m resolution to reduce the computational cost of running a model in such a large landscape. After resampling the warbler density map to a hexagonal grid for use in HexSim, the density values ranged from 0.001-1.0383 males/ha, which did not change significantly from the original 10-m raster (0.001-1.049 males/ha). The resulting hexagonal density map had a hexagon width of 100-m and the area of each hexagon was 0.866 ha. The values of this density map were used as a representation of habitat quality. To parameterize some of the life cycle events in our model, we translated the density model values into four habitat categories: low (< 0.0625 males/ha), marginal (0.0625-0.16 males/ha), moderate (0.16-0.25 males/ha), and optimal (>0.25 males/ha).

Movement

We modeled the life cycle to include two movement events. The first movement event represented breeding dispersal and was set to occur at the beginning of the annual cycle and applied only to adults (age ≥ 1) to signal breeding dispersal. The second movement event occurred after reproduction, which applied only to juveniles and represents natal dispersal (Figure 2.1). Each movement event included two main steps: dispersal and exploration. For both adults and juveniles, the individual dispersed a certain number of hexagons, guided with 80% autocorrelation, towards higher valued hexagons. The total number of dispersal steps any individual took depended on a stopping criterion that averaged the density values of each hexagon it passed through over a determined path length. Once an individual reached the target average value, the individual stopped moving and moved onto the exploration step. For adults, we allowed individuals to move two steps first, and then if the next two steps averaged higher than 0.06, they stopped moving. Juveniles, because natal dispersal events are generally longer than inter-year breeding dispersal events, they moved 15 steps first and then took five steps to calculate and reach or supersede the average density value of 0.06 required for exploration (Jette et al. 1998, Lindsay et al. 2008). The number of steps individuals took was tallied. If the defined maximum distance was reached, the individual stopped moving.

After dispersal, individuals explored the surrounding area to determine if a territory could be made. We parameterized the model to allow both adults and juveniles to explore 69 hexagons (or 60 ha) surrounding the hexagon to which they dispersed. If an individual explored and found a territory, it could then reproduce. Otherwise, the individual would become a non-breeding "floater" and would have to attempt to find a territory in the following timestep, unless they died during the survival event. To increase the probability of finding a territory, the movement event was repeated up to five times stopping when the individual found a territory, reached the maximum dispersal distance, or concluded the five iterations, whichever came first. For adults, the maximum dispersal distance was set to 3,400 m, based on records from Fort Cavazos (Groce et al. 2010). For juveniles, the maximum dispersal distance was set to 114,000 m, based on records from BCP and the Joint Base San Antonio Camp Bullis. However, few individuals traveled the maximum distance due to the iterative parameterization of dispersal and exploration. The parameterization of the movement events took extensive parameter tuning to achieve the average dispersal rates that match empirical data.

Territory Selection

To create a territory, simulated male warblers needed to find enough hexagons with habitat quality values that summed to 1. Territory size could start at one hexagon, but we parameterized the model to have a maximum territory size of 23.094 hexagons or 20 hectares, based on the largest territory size recorded in low-density sites at the Balcones Canyonlands Preserve in Austin, Texas (O'Donnell et al. 2019). The model resulted in an average territory size of 6.01 ha. Average territory sizes were 15.7 ha (12.7-19.9 ha), 8.3 ha (6.1-15.6 ha), 4.8 ha (4.3-6.9 ha), and 3.3 ha (0.9-4.3 ha) in low, marginal, moderate, and optimal, respectively. The range of simulated territory sizes matched the territory sizes from empirically based estimates in literature (Coldren 1998, Reidy et al. 2016, Pulich 1976, Davis and Leslie 2008).

Reproduction

For the reproduction event, only territory-holding adults were allowed to reproduce (Figure 2.1). We set reproduction to allow territory-holders to have a maximum of three offspring. The typical warbler clutch size is 3-4 eggs (Pulich 1976). Based on existing literature, we parameterized our model to result in an average of 1.45 successful fledglings per male (Duarte et al. 2016, Groce et al. 2010). To achieve this target average, the probabilities of having one, two or three fledglings were set to 0.65, 0.25, and 0.1, respectively. We parameterized this part of the model based on a study that estimated reproductive success as 1.42 (95% CI 1.18-1.69) fledglings per territory (Duarte et al. 2016). Multiple other studies had similar or relatively higher estimates of reproductive success (Peak and Thompson 2014, Reidy et al. 2018, Reidy et al. 2020, Reidy et al. 2023, Groce et al. 2010). After the reproduction event, fledglings became juveniles that could disperse and search for territories in their own movement event (Figure 2.1).

Survival

We based our survival rates on empirical data from Reidy et al. (2020) and Duarte et al. (2016). However, multiple other studies have found similar rates (Alldredge et al. 2004, Reidy et al. 2023). Reidy et al. (2020) estimated mean juvenile survival to be 0.40 and mean adult survival to be 0.57 for the Balcones Canyonlands Preserve. For floaters, we assigned these means to the moderate habitat quality category because the Preserve is made up of moderate and optimal habitat. We then reduced and increased this value by 30% to assign values to low, marginal and optimal habitat elsewhere in the landscape. To address floaters' reduced access to resources, we imposed a 40% penalty on the survival rates of each of the habitat quality categories.

The habitat quality categories are based on the average quality of the hexagons in a territory. This means that even having a territory with one very low-quality hexagon with majority moderate to optimal quality hexagons could result in a territory with a lower habitat quality category than would be expected. Using territory size for survival rates provided a more accurate representation of resource access than using the coarser habitat quality categories. Therefore, for territory-holding individuals, the survival rates were linearly extrapolated based on territory size. Using data from Duarte et al. (2016), survival rates for adults ranged from 0.29 to 0.73 for the smallest and the largest territories, respectively. For territory-holding juveniles, the survival rates ranged from 0.07 to 0.52 for the smallest to the largest territories. After iterative tuning, our final model produced mean juvenile and adult survival rates of 0.31 and 0.59, respectively. These rates accurately represent empirical data across study sites (Alldredge et al. 2004, Duarte et al. 2016, Reidy et al. 2020, Reidy et al. 2018, Reidy et al. 2023). Adults older than 10 years were removed from the simulation past a decade, matching empirical data that found the oldest individual on record to be approximately 11 years old (Colon et al. 2015, Ladd and Gass 1999).

Model Initialization

Warbler abundance has been widely debated. Pulich (1976) first estimated the population to total to about 14,950 individuals in 1976, but Wahl et al. (1990) later estimated the carrying capacity to be between 4,822 to 16,016 pairs based on data from 1974, 1976 and 1981. However, Morrison et al. (2010) estimated the population to be 220,000 males in 2009 and Mathewson et al. (2012) estimated it to be 263,339 males based on data from 2008 and 2009. The density model used to create a relationship between density, habitat quality, and demographics in this simulation model estimated a similar population size of 217,444 males. Previous research comparing model-based densities to actual densities from intensive territory monitoring found that various modeling methods (e.g., binomial mixture models, distance sampling) consistently overestimate densities in areas of low density and underestimate in areas of high density (O’Donnell et al. 2019). O’Donnell et al. (2019) did not, however, assess the methodologies used in the Mueller et al. (2022) density model. Nevertheless, given the uncertainties in both modeled and actual warbler abundance, we focused on comparing relative abundance among scenarios rather than making population size estimates.

In our model, initialization occurred on the first timestep. We randomly introduced 100,000 male warblers into the landscape, which immediately triggered an exploration event in which individuals were able to explore their location and find a territory. If any individuals were unable to create a territory, they were allowed to try again in the movement event (Figure 2.1). The model was run for 70 years with the chosen parameters to determine the timestep in which the population stabilized. We used the calibrated population as a starting point for all of the climate-change scenario simulations.

To determine if the number of individuals used to initialize the model affected resulting abundances, we initialized the model using six different population sizes: 15,000, 30,000, 90,000, 100,000, 200,000, and 300,000. Regardless of the number of individuals used to initialize the model, it simulated populations between 78,160 and 78,883 males by timestep 70. This means that our selected model stabilized at a similar abundance regardless of how the simulation was initialized, and therefore, was not overly sensitive to initialization abundance.

Simulation Scenarios

To produce a baseline scenario, we ran the model using the Mueller et al. (2022) density model-based habitat layer, representing habitat in the year 2020. In the baseline scenario, the habitat map remained unchanged for all years. To evaluate the risk of resource loss to warbler populations, we used four scenarios of habitat change that incorporated projections from an ensembled Ashe juniper species distribution model (SDM). This SDM was run for four projected future climates from two generalized circulation models (GCMs) run for two shared socioeconomic pathways (SSPs) for the time periods 2021-2040, 2041-2060, 2061-2080, and 2081-2100 (Santillana Fernandez et al. *In prep*). The GCMs included the Max Planck Institute Earth System Model (MPI-ESM1-2-HR) and the U.K. Earth System Model (UKESM1-0-LL) (Gutjahr et al. 2019, Yukimoto et al. 2019, Sellar et al. 2019). These GCMs were selected using *GCMeval* tool created by Parding et al. (2020), which assesses model fit to past conditions based on selected parameters (e.g., region, importance of precipitation or temperature).

MPI-ESM1-2-HR represents a negligible change in precipitation with a moderate increase in temperature, while the UKESM1-0-LL forecasts a significant increase in both temperature and precipitation. The SSPs used for these GCMs were SSP2-4.5 and SSP3-7.0. SSP2-4.5 (middle-of-the-road) is a scenario that aims to implement a limit of warming to approximately 3˚C by 2100. While similar to SSP2-4.5, SSP3-7.0 (regional rivalry) projects a more extreme climate scenario with increased land-use change and high aerosol emissions (O'Neill et al. 2016). Santillana Fernandez et al. (*In prep*) used the SDM to project changes in the distribution of Ashe juniper for each of the four time periods for the four climate scenarios.

We took the projected distribution maps from (Santillana Fernandez et al. *In prep*) and interpolated between the four time periods to create yearly habitat maps from 2021-2090. Each of the Ashe juniper distribution projections was binarized by applying a presence threshold (Santillana Fernandez et al. *In prep*). We then used the yearly binarized maps to modify the map produced by the Mueller et al. (2022) warbler density model by retaining only areas that were projected to be suitable for Ashe juniper as potential warbler habitat.

To capture stochasticity inherent in the model, each simulation scenario (the baseline scenario and the four climate-change scenarios) was run 10 times. Because variation in model projections was minimal, 10 replicates were more than enough to capture any differences resulting from the stochastic elements in the model. For example, across baseline model replicates, the average populations in 2021 and 2090 were 86,978 males and 86,275 males, respectively. Furthermore, across all model scenarios, the standard deviation did not exceed 460 individuals in any given year. This was expected because although the model contains stochastic elements, we did not explicitly incorporate environmental stochasticity into the model.

Assessing Changes on Protected Lands

Because the majority of the land within the warbler breeding range is privately owned, assessing the impact of climate-induced resource loss on protected or actively monitored areas was an additional goal of our study. We focused on sites that had historical warbler data to support our model parameterization. These protected areas included Albert & Bessie Kronkosky State Natural Area (ABKSNA), Balcones Canyonlands National Wildlife Refuge (BCNWR), Balcones Canyonlands Preserve (BCP), Fort Cavazos (FC), Garner State Park (GSP), Government Canyon State Natural Area (GCSNA), Guadalupe River State Park (GRSP), Hill Country State Natural Area – Louise Merrick Unit (HCSNALMU), Honey Creek State Natural Area (HCSNA), Inks Lake State Park (ILSP), Longhorn Cavern State Park (LCSP), Pedernales Falls State Park (PFSP), and South Llano River State Park (SLRSP), which all actively manage or monitor warbler habitat (Figure 2.1). The majority of these sites are protected for conservation purposes and recreational use, but some are actively monitored sites that have alternative purposes such as the Fort Cavazos military installation. Hereafter, we refer to all of these sites that actively monitor warbler populations as protected areas. We used the warbler habitat projections to determine the relative changes in the warbler population under the different climate scenarios.

RESULTS

Range-wide projected abundance changes

The baseline scenario resulted in a stable population over the seventy-year simulation period (Figure 2.3). Although the baseline scenario used the existing Mueller et al. (2022) density model as its spatial extent, simulated warblers did not occupy the entire range. The areas of the range that were occupied in the baseline scenario are shown in gray in Figure 2.4 to provide a comparison for the future climate scenarios.

Warbler populations declined under all four climate-change scenarios. However, the degree to which they declined varied greatly. Under the MPI-ESM1-2-HR SSP2-4.5 scenario (the scenario resulting in the least climatic change), the population remained stable with a gradual and slight decline. By 2090, that decline resulted in an 11% loss in the population relative to the baseline scenario (Figure 2.3). In this scenario, warblers occupied the landscape similarly to the occupancy pattern created by the baseline scenario with the highest cumulative occupancy in the central region of the Edwards Plateau, and near the cities of Austin and Killeen (Figure 2.4a). In this scenario, warblers continued to occupy low quality habitat in high numbers. Under the SSP3-7.0, the MPI-ESM1-2-HR model showed the warbler population responding similarly to the SSP2-4.5 projection until approximately 2060 when the population rapidly declined (Figure 2.3). In comparison to the baseline model, this scenario predicted a 51% reduction in the population by 2090. Although warbler occupancy persisted in the same crucial regions as projected by the SSP2-4.5 scenario, occupancy of low and marginal quality hexagons declined the most in comparison to the other habitat quality categories (Figure 2.4b).

Projections from the UKESM1-0-LL model, run for both the SSP2-4.5 and SSP3-7.0 scenarios resulted in similar population responses with an almost immediate yet gradual decline that plateaued by approximately 2070 (Figure 2.3). In comparison to the baseline model, we observed a 94% reduction in the population by 2090 under both of these scenarios. This severe population reduction left warblers concentrated mainly around the wooded areas near the cities of Austin and Killeen (Figure 2.4c and 2.4d). However, few warblers occupied the rest of the baseline range except for some minimal use in the southeastern part of the Balcones Escarpment, which also had slightly higher occupancy rates under the SSP3-7.0 scenario than the SSP2-4.5.

We averaged our warbler abundance projections for each of the SSP scenarios (Figure 2.3). The average for the SSP2-4.5 scenarios showed an immediate drop in the population followed by a gradual decrease in the population, which appeared to plateau below 50,000 males at around 2060. In this average, the projected population declined in a similar fashion to the UKESM1-0-LL models but did not lead to such an extensive loss of the population. In comparison to the baseline scenario, the SSP2-4.5 average predicted about a 52% decline in the warbler population by 2090. The average for the SSP3-7.0 scenarios showed an immediate drop in the population similar to the SSP2-4.5 average but showed a nearly linear decline in the population through 2090. Based on the trend of this SSP3-7.0 average, there appeared to be no indication that the population would plateau at any time after 2090. By the end of the century, for this average, the population declined by about 73% in comparison to the baseline scenario.

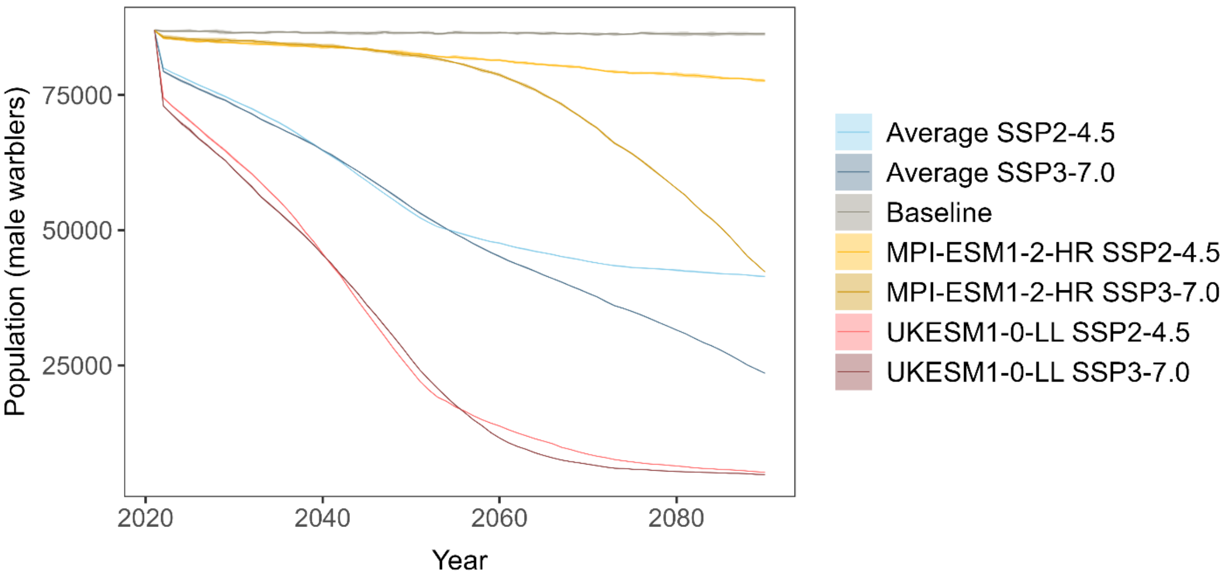

Figure 2.3 Simulated Golden-cheeked Warbler populations for baseline conditions and for each of the four climate-change scenarios. Under the most extreme GCM, UKESM1-0-LL, the population declines to near extinction by 2090. The SSP2-4.5 and SSP3-7.0 scenarios were averaged to provide a summary of the two distinct projections of socioeconomic global change. Although the model is built to be stochastic, the population did not vary significantly across replicates (n = 10). The standard deviation around the mean was plotted for every scenario, with the standard deviation staying within 27 and 460 male warblers.

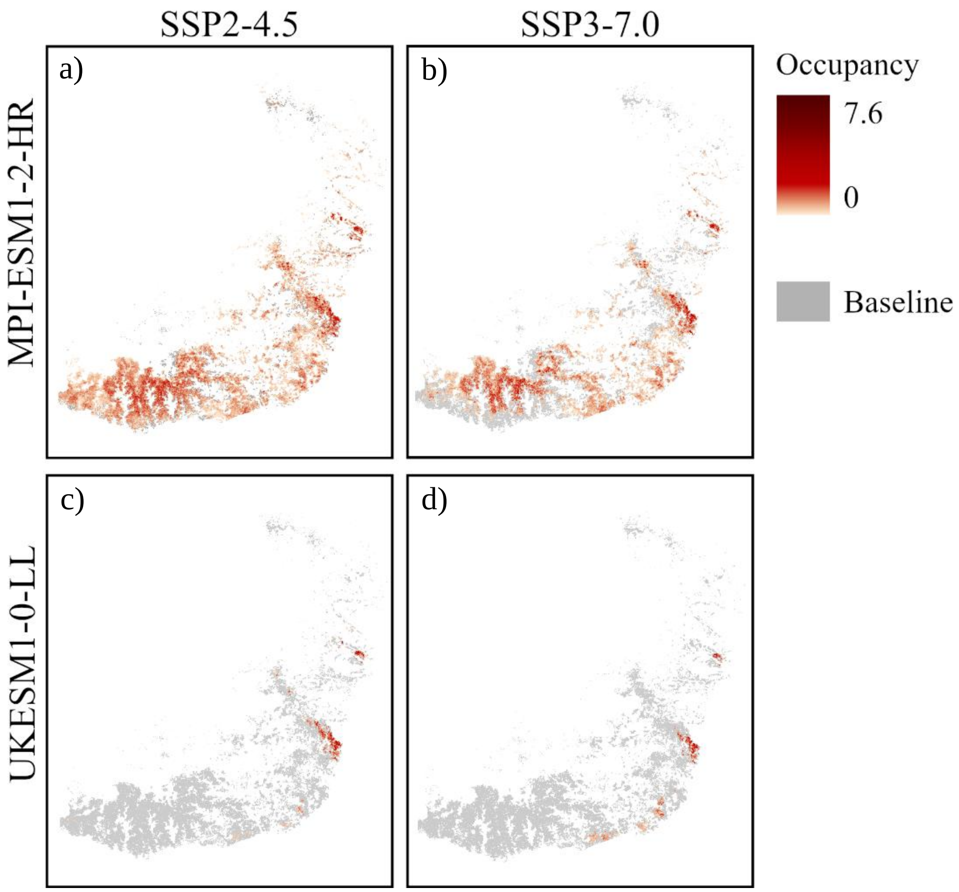

Figure 2.4 Average cumulative occupancy from 2080 to 2090 by Golden-cheeked Warblers resulting from simulations run for four climate-change scenarios. The gray background provides a reference of the extent of occupancy under the baseline model.

Projected abundance within protected lands

We assessed the change in occupancy across selected protected areas within the warbler's current range between 2020 and 2090. The protected lands we used account for 1,289 km^2 of approximately 68,000 km^2 of the warbler's current breeding range. The pattern of population change across all climate scenarios was similar between protected and unprotected areas, with the occupancy change in protected areas being lower than in unprotected areas. For example, in the MPI-ESM1-2-HR SSP2-4.5 scenario, protected areas experienced at least a 4% loss of the population whereas unprotected areas experienced approximately a 12% reduction in the population (Figure 2.5). In the most extreme scenario (UKESM1-0-LL), protected areas experienced a 70% reduction in the population whereas unprotected areas lost nearly 97% of the population.

However, the pattern of where the persisting population was located depended on the climate scenario. In the MPI-ESM1-2-HR SSP2-4.5 scenario, about 82% of the population occupied unprotected areas in 2090. A similar pattern occurred in the SSP3-7.0 scenario of this GCM with approximately 79% of the population in unprotected land. This pattern was the opposite in the UKESM1-0-LL scenarios. In the UKESM1-0-LL SSP2-4.5 scenario, 59% of the persisting population occupied protected areas. Similarly, in the UKESM1-0-LL SSP3-7.0 scenario, roughly 50% of warblers occupied protected lands in 2090. Thus, under these more extreme scenarios, warblers disproportionately occupied the protected areas which account for less than 2% of the warbler's current breeding range.

For the mildest climate scenario, MPI-ESM1-2-HR SSP2-4.5, all protected areas continued to host warbler populations until 2090 with the largest average loss (80%) happening at SLRSP (Figure 2.6). All areas saw little to no reduction in the population except for HCSNA and LMSNA, which saw averages of 7% and 1% population increases under this scenario. In the MPI-ESM1-2-HR SSP3-7.0 scenario, four out of the 14 sites—LCSP, PFSP, SLRSP, and ILSP—saw a complete loss of warbler occupancy by 2090. The sites that saw less than 20% loss were ABKSNA (2%), BCP (8%), BCNWR (19%), GCSNA (7%), and LMSNA (13%), suggesting these are the most important protected sites for this scenario.

For the UKESM1-0-LL model projections, the SSP3-7.0 scenario resulted in less of a population reduction than did the SSP2-4.5, but the outcome was relatively the same for protected areas (Figure 2.6). Under SSP2-4.5, 11 out of the 14 sites experienced a complete loss in warbler occupancy by 2090, whereas the SSP3-7.0 scenario saw a complete loss in 9 out of 14 of the sites. Of the five sites that persisted under the UKESM1-0-LL SSP3-7.0 scenario, GCSNA consistently hosted a considerable portion of the population (approximately 4%) across all model replicates even though it experienced an average occupancy loss of 63% by 2090. However, in the SSP2-4.5 scenario of this GCM, both GCSNA and ABKSNA hosted less than 0.1% of the population, with some model replicates experiencing complete loss of warbler occupancy within these sites.

There were three protected areas in which warblers persisted even under the most extreme climate-change scenarios: BCP, BCNWR and FC. These sites are the largest protected or actively managed areas where the majority of warbler research has been conducted. All model runs hosted remnant populations within these sites across all climate scenarios. For the most extreme climate model (UKESM1-0-LL), these three sites continue to sustain warblers, but at much lower numbers. Under the UKESM1-0-LL SSP2-4.5 scenario, the populations at BCP, BCNWR and FC all experienced moderate population reductions (28%, 61%, and 66%, respectively). In this scenario, by 2090, BCP hosted about 35% of the remnant population whereas BCNWR and FC hosted approximately 11% and 16%, respectively. Under the UKESM1-0-LL SSP3-7.0 scenario, the population reduction was most severe at BCNWR (-92%) and moderate to high at BCP (-40%) and FC (-78%). By 2090, this scenario showed that BCP hosted about 32% of the remnant population whereas BCNWR and FC hosted only 2% and 12%, respectively. The simulation model detected important regions within these three sites that managers could prioritize during conservation planning efforts (Figure 2.7).

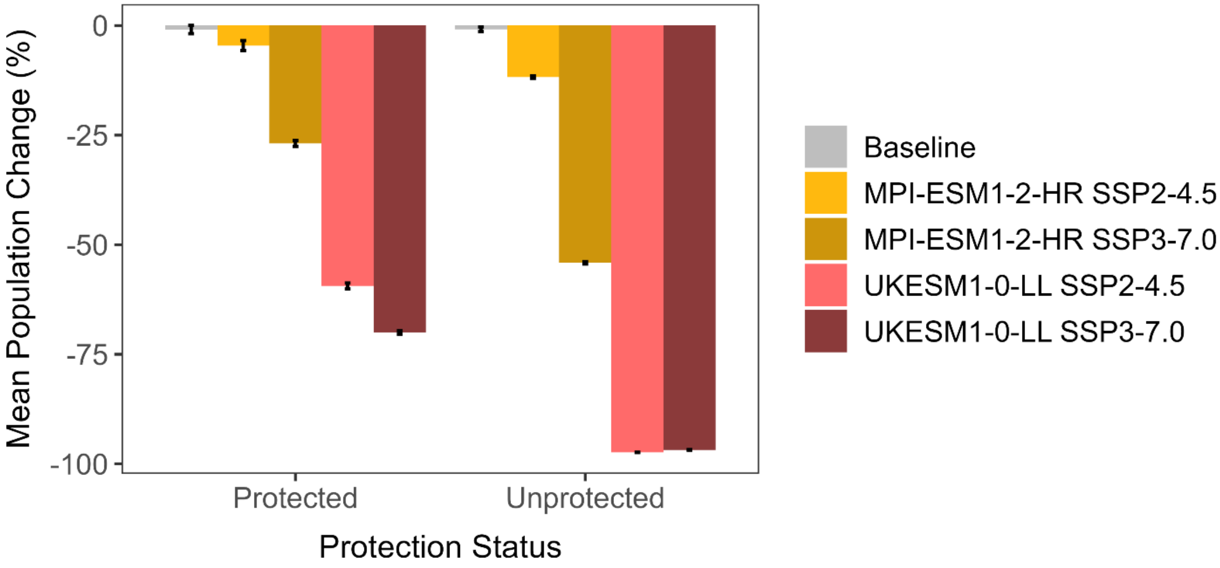

Figure 2.5 Mean change in the simulated male warbler population for the protected land versus unprotected lands between year 2020 and year 2090. The change was calculated for the baseline scenario and the four climate scenarios with the error bars representing the variability across model runs. The UKESM1-0-LL climate scenarios (both SSP2-4.5 and SSP3-7.0) showed at most 70% loss of population in protected lands, while in unprotected lands, this GCM showed nearly a 97% loss of the population. Although the pattern of loss across scenarios was similar for protected versus unprotected lands, the population that persists through 2090 in the more extreme scenarios mainly occupies protected sites rather than unprotected lands.

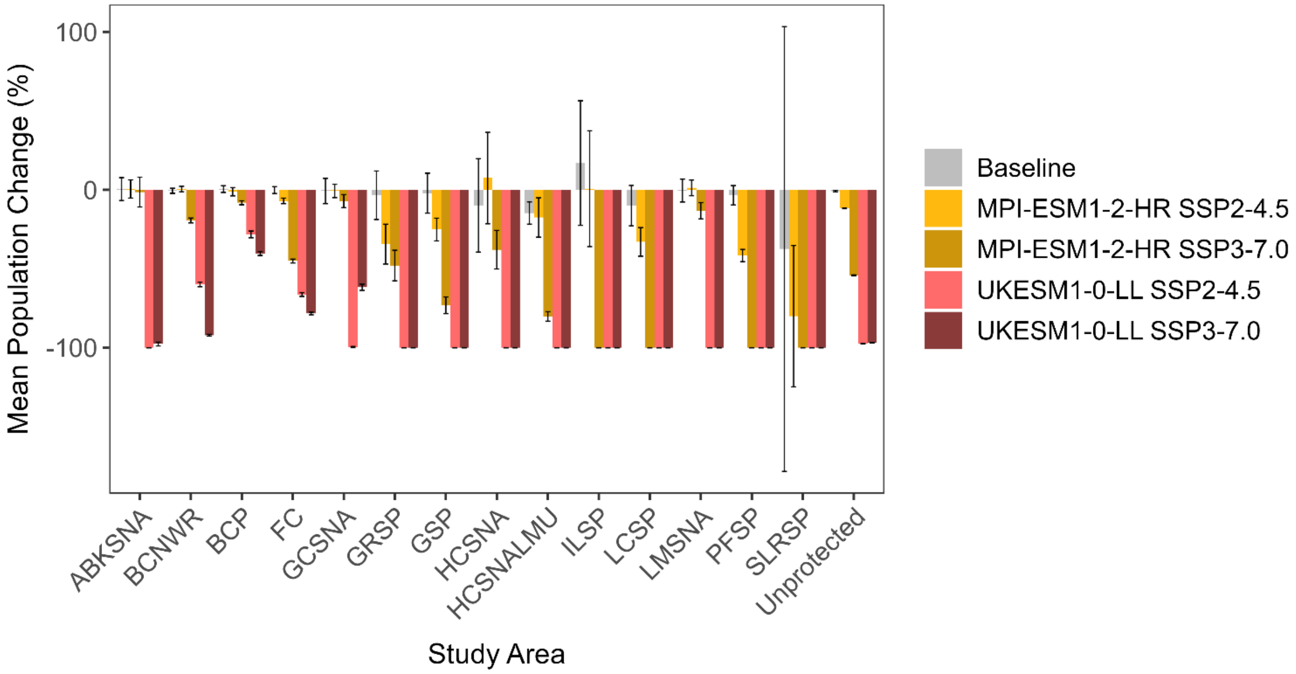

Figure 2.6 Mean change in the simulated male warbler population for each of the protected or managed sites between year 2020 and year 2090. The change was calculated for the baseline scenario and the four climate scenarios with the UKESM1-0-LL climate scenarios (both SSP2-4.5 and SSP3-7.0) showing nearly a 100% loss of population at all sites except for BCNWR, BCP, Fort Cavazos and GCSNA. The error bars represent the SD of the mean occupancy across model replicates (n = 10). Smaller sites had more variability in occupancy.

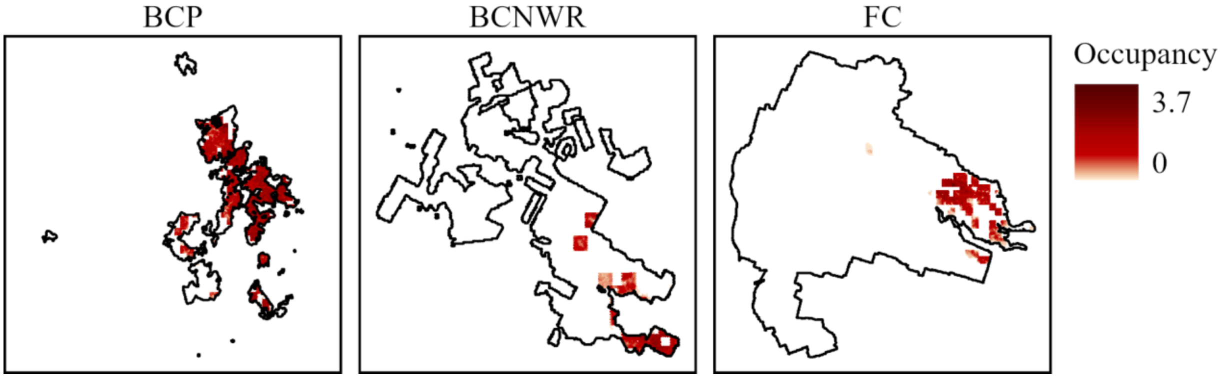

Figure 2.7 Average cumulative occupancy from 2080 to 2090 by Golden-cheeked Warblers at the three protected sites where they persist for the most extreme climate scenario (UKESM1-0-LL SSP3-7.0).

DISCUSSION

Forecasting the impacts of climate change and habitat change is essential for planning and prioritizing effective conservation efforts for at-risk species in the face of environmental change. We built a spatially explicit population model to assess the potential impact of climate-induced resource loss on the endangered Golden-cheeked Warbler. We found that projected climate-driven reductions in the distribution of Ashe juniper have the potential to substantially impact warbler populations. Nonetheless, there were specific areas in which warblers are likely to persist.

Our results highlighted three protected sites that have the potential to serve as refugia for the warbler. Warblers persisted at these sites even under the most severe climate scenario we considered. Morelli et al. (2016) define climatic refugia as areas relatively buffered from climate change that enable persistence of valued physical, ecological, and socio-cultural resources. The areas of persistence at the three sites we identified (Fig. 7) had projected climatic conditions that allowed for the persistence of Ashe juniper, which in turn provided adequate habitat to support warblers.

Conserving and restoring areas that will serve as refugia is likely to be an important climate-adaptation strategy for protecting species and ecosystems in the face of climate change (McLaughlin et al. 2022). The warbler is already being managed at the sites that are likely to host refugia. For example, at BCNWR and Fort Cavazos, understory thinning and prescribed fires have been implemented or studied as a strategies to reduce fuel loads and diminish the risk of crown fires in mature juniper-oak woodlands (Long et al. 2017, Reidy et al. 2021, Reemts et al. 2024). Additionally, with the importance of oaks to warbler foraging behavior, habitat management that focuses on the protection of both Ashe juniper and oak species will be essential. With deer herbivory reducing oak regeneration, studies have focused on assessing strategies (e.g., planting, low-intensity fire) that could improve oak resprouting and seedling survival in a way that also maintains juniper on the landscape (O'Donnell et al. 2020, Andruk and Fowler 2015). Therefore, by protecting existing juniper-oak woodlands and associated successional communities, reducing fire risk, increasing connectivity, and promoting oak regeneration, managers could reduce the impact of habitat and resource loss on warbler populations, effectively protecting important climate refugia.

As with any model projections, caution should be taken in interpreting and using the results of our model in planning. There is at least one reason why our projections might overestimate the impacts of climate change on warbler populations. Our projected changes in habitat resulting from juniper range contraction assume that existing junipers will die immediately in areas that the species distribution model projects to be unsuitable. Although this is possible, it is also possible that at least some mature trees will remain on the landscape for many years, particularly if the lack of suitability is only linked to recruitment. Such a lag in juniper mortality would reduce the rate of population decline and could result in larger warbler populations. Conversely, there are reasons that our model might under-predict the impact of climate change. It is possible that the compounding effects of climate-mediated disturbances (e.g. drought, wildfire) and land-use change could produce a more substantial decline in both juniper suitability and warbler habitat availability.

Previous research has shown that both drought and fire can reduce the resilience of junipers and juniper-oak woodlands. For example, in 2011, a severe drought resulted in mass tree mortality throughout Texas, especially impacting juniper-oak woodlands (Moore et al. 2016, Schwantes et al. 2017). Slow growing trees faced a high risk of mortality with some studies predicting that future severe droughts will lead to severe mortality risk and dynamic water stress for mature Ashe junipers (Polley et al. 2018, Schwantes et al. 2018). Although it is possible that the species distribution model we used implicitly captured drought events, we did not explicitly include these in our simulations. It is possible that including such events could further reduce warbler populations.

Similarly, although the species distribution model could potentially implicitly capture the effects of climate change on fire and in turn on the distribution of juniper, we did not explicitly model the impacts of climate-change driven changes to the fire regime and the resulting impacts on warbler habitat. Climate-driven increases in the severity and frequency of wildfires in Texas will likely increase the possibility of devastating crown fires (Gao et al. 2021, Nielsen-Gamon et al. 2021). In the past, Indigenous stewardship and burning practices, along with the role of bison and other browsing animals, maintained the mosaic of savannas, shrublands and woodlands of this region (Fowler and Carden 2024, Stambaugh et al. 2014, Stambaugh et al. 2017). Since

European settlement, fire suppression has resulted in changes to the successional dynamics and composition of the ecosystems of central Texas, resulting in high fuel loads and high fire risk. As a non-resprouting species that may take at least 75 years to recolonize, Ashe juniper may experience substantial loss in its distribution if faced with increased exposure to fire, reducing the suitability and distribution of warbler habitat (Fuhlendorf et al. 1996, Fowler and Carden 2024, Reemts et al. 2024).

Studies assessing the impacts of prescribed fire and wildfire on warblers found that the use of habitat declined considerably after fire, especially in areas of crown mortality (Baccus et al. 2007, Reidy et al. 2021, Reemts et al. 2024). Additionally, fledgling survival has also been found to be lower in prescribed fire treatment sites, suggesting that fire could have significant effects on survival and reproduction. A recently published model found that adult male survival was negatively related to El Niño severity further emphasizing this relationship between demographic rates and bioclimatic conditions (Reidy et al. 2023). In our model, survival was kept constant throughout the years of landscape change for the purpose of simplicity. The additive or synergistic effects of climate change, fire, and drought are likely to induce significant landscape changes and phenological shifts that will affect interspecific and intraspecific interactions, migration, and survival of this at-risk species (Cox et a. 2013, Marshall et al. 2013, Peak and Thompson 2014, Reidy et al. 2021). Explicitly including these mechanisms in our model would likely result in more dramatic population declines.

In addition, extensive research has documented the negative effect of urbanization and land development on the quantity and quality of warbler habitat, as well as warbler demographics (Dreiss et al. 2022, Groce et al. 2010, Appel & Camilli 2010). A recently published technical report developed an analysis on the impact of projected land-cover change on the warbler breeding range (Bunting 2023). The results of this report showed that the most vulnerable areas are spread along the Balcones Escarpment and the eastern sections of the breeding range, which are the same areas in which our model predicts persistence. Thus, protecting habitat from development and other forms of land conversion in these areas is likely to be critical for the persistence of the warbler.

In early 2025, the U.S. Fish and Wildlife Service (USFWS) published their five-year status review for the Golden-cheeked Warbler and recommended the species be downlisted to threatened (USFWS 2025). The original decision to list the warbler as endangered was based largely on the substantial loss and fragmentation of warbler breeding habitat. However, the recent review indicated that the species has sufficient high density breeding habitat available and plenty of low to medium density habitat that will ultimately mature into high-density habitat. Although downlisting could be justified given their assessments, the review did not consider the potential impact of climate change on Ashe juniper. Under the most extreme climate scenarios, our model showed warbler occupancy declined rapidly early in the century and warblers disappeared almost entirely by the end of the century—all due to the species' obligate dependence on Ashe juniper. Our results indicate that climate is likely to be an important stressor that affects species viability and this assessment, or the associated framework, could be used by managers in subsequent species status assessments. Regardless of the species' status, it will be essential to continue monitoring warbler populations as well as managing juniper-oak woodlands with the aim of protecting old-growth junipers and promoting oak regeneration. Our results emphasize the continued need to implement effective conservation and climate mitigation strategies to secure the persistence of both the Golden-cheeked Warbler and Ashe juniper through the end of the century.

REFERENCES

Adams-Hosking, C., C. McAlpine, J. R. Rhodes, H. S. Grantham, and P. T. Moss. 2012. Modelling changes in the distribution of the critical food resources of a specialist folivore in response to climate change. Diversity and Distributions 18:847–860.

Alldredge, M. W., J. S. Hatfield, D. D. Diamond, and C. D. True (2004). Golden-cheeked Warbler (Dendroica chrysoparia) in Texas: Importance of dispersal toward persistence in a metapopulation. In Species Conservation and Management: Case Studies (H. R. Ak¸cakaya, M. A. Burgman, O. Kindvall, C. C. Wood, P. Sjogren-Gulve, J. S. Hatfield, and M. A. McCarthy, ¨ Editors). Oxford University Press, New York, NY, USA. pp. 372– 383.

Andruk, C. M., and N. L. Fowler. 2015. Conflicting short and long-term management goals: Fire effects in endangered golden-cheeked warbler (Setophaga chrysoparia) habitat. In: Keane, Robert E.; Jolly, Matt; Parsons, Russell; Riley, Karin. Proceedings of the large wildland fires conference; May 19-23, 2014; Missoula, MT. Proc. RMRS-P-73. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. p. 22-29. 73:22–29.

Appel, D. N., and K. S. Camilli. 2010. Assessment of oak wilt threat to habitat of the golden-cheeked warbler, an endangered species, in central Texas. In: Pye, John M.; Rauscher, H. Michael; Sands, Yasmeen; Lee, Danny C.; Beatty, Jerome S., tech. eds. 2010. Advances in threat assessment and their application to forest and rangeland management. Gen. Tech. Rep. PNW-GTR-802. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest and Southern Research Stations: 61-71 802:61–71.

Baccus, J. T., J. D. Cornelius, M. E. Tollé, and Texas Ornithological Society. 2007. Response of golden-cheeked warblers (Dendroica chrysoparia) to wildfires at Fort Hood, Texas. Texas Ornithological Society, [San Antonio, Tex.]:7

Bateman, B. L., C. Wilsey, L. Taylor, J. Wu, G. S. LeBaron, and G. Langham. 2020. North American birds require mitigation and adaptation to reduce vulnerability to climate change. Conservation Science and Practice 2:e242.

Bellard, C., C. Bertelsmeier, P. Leadley, W. Thuiller, and F. Courchamp. 2012. Impacts of climate change on the future of biodiversity. Ecology Letters 15:365–377.

Both, C., M. Van Asch, R. G. Bijlsma, A. B. Van Den Burg, and M. E. Visser. 2009. Climate change and unequal phenological changes across four trophic levels: constraints or adaptations? Journal of Animal Ecology 78:73–83.

Bunting, D. 2023. Land Use Land Cover Change Modeling and Change Projections across the Golden-cheeked Warbler Breeding Range. Science Applications, U.S. Fish and Wildlife Service. Technical Report. pp 63.

Coldren, C. L. 1998. The effects of habitat fragmentation on the golden-cheeked warbler. Dissertation, Texas A&M University, College Station, Texas, USA.

Colón, M. R., R. S. Holden, and M. L. Morrison. (2015). Golden-cheeked Warbler: New maximum longevity record. Western Birds 46:261-262.

Cox, W. A., F. R. Thompson III, and J. L. Reidy. 2013. The Effects of Temperature on Nest Predation by Mammals, Birds, and Snakes. The Auk 130:784–790.

Crouchet, S. E., J. Jensen, B. F. Schwartz, and S. Schwinning. 2019. Tree Mortality After a Hot Drought: Distinguishing Density-Dependent and -Independent Drivers and Why It Matters. Frontiers in Forests and Global Change 2.

Davis, C. A., and D. M. Leslie, Jr. 2008. Effects of mountain biking activity on foraging and nesting behavior of golden-cheeked warblers, Final report. Department of Natural Resource Ecology and Management, University of Oklahoma.

Dreiss, L., P. Sanchez-Navarro, and B. Bird. 2022. Spatiotemporal patterns in Golden-cheeked Warbler breeding habitat quantity and suitability. Avian Conservation and Ecology 17:art14.

Duarte, A., J. L. R. Jensen, J. S. Hatfield, and F. W. Weckerly. 2013. Spatiotemporal variation in range-wide Golden-cheeked Warbler breeding habitat. Ecosphere 4:1–12.

Duarte, A., F. W. Weckerly, M. Schaub, and J. S. Hatfield. 2016. Estimating golden-cheeked warbler immigration: implications for the spatial scale of conservation. Animal Conservation 19:65–74.

Farrell, S. L., B. A. Collier, K. L. Skow, A. M. Long, A. J. Campomizzi, M. L. Morrison, K. B. Hays, and R. N. Wilkins. 2013. Using LiDAR-derived vegetation metrics for high-resolution, species distribution models for conservation planning. Ecosphere 4:art42.

Fortini, L. B., and K. Dye. 2017. At a global scale, do climate change threatened species also face a greater number of non-climatic threats? Global Ecology and Conservation 11:207–212.

Fowler, N. L., and R. E. Carden. 2024. Roles of fire in the plant communities of the eastern Edwards Plateau of Texas. Fire Ecology 20:55.

Fuhlendorf, S. D., F. E. Smeins, and W. E. Grant. 1996. Simulation of a fire-sensitive ecological threshold: a case study of Ashe juniper on the Edwards Plateau of Texas, USA. Ecological Modelling 90:245–255.

Gao, P., A. J. Terando, J. A. Kupfer, J. Morgan Varner, M. C. Stambaugh, T. L. Lei, and J. Kevin Hiers. 2021. Robust projections of future fire probability for the conterminous United States. Science of The Total Environment 789:147872.

Groce, J., Mathewson, H., Morrison, M., and N. Wilkins. 2010. *Scientific evaluation for the 5-year status review of the golden-cheeked warbler* (Section 6 (Texas Traditional) Report Review Au TX E-102-R).

Gutjahr, O., D. Putrasahan, K. Lohmann, J. H. Jungclaus, J.-S. von Storch, N. Brüggemann, H. Haak, and A. Stössel. 2019. Max Planck Institute Earth System Model (MPI-ESM1.2) for the High-Resolution Model Intercomparison Project (HighResMIP). Geoscientific Model Development 12:3241–3281.

Heinrichs, J. A., D. J. Bender, and N. H. Schumaker. 2016. Habitat degradation and loss as key drivers of regional population extinction. Ecological Modelling 335:64–73.

Hitch, A. T., and P. L. Leberg. 2007. Breeding Distributions of North American Bird Species Moving North as a Result of Climate Change. Conservation Biology 21:534–539.

Jette, L. A., T. J. Hayden, and J. D. Cornelius. 1998. Demographics of the Golden-cheeked Warbler (Dendroica chrysoparia) on Fort Hood, Texas.

Johnson, D. M., J.-C. Domec, Z. Carter Berry, A. M. Schwantes, K. A. McCulloh, D. R. Woodruff, H. Wayne Polley, R. Wortemann, J. J. Swenson, D. Scott Mackay, N. G. McDowell, and R. B. Jackson. 2018. Co-occurring woody species have diverse hydraulic strategies and mortality rates during an extreme drought. Plant, Cell & Environment 41:576–588.

Ladd, C., and L. Gass. 1999. Golden-cheeked Warbler (Setophaga chrysoparia), version 1.0. Birds of the World.

Lawler, J. J., S. P. Campbell, A. D. Guerry, M. B. Kolozsvary, R. J. O’Connor, and L. C. N. Seward. 2002. The Scope and Treatment of Threats in Endangered Species Recovery Plans. Ecological Applications 12:663–667.

Li, R., M. Xu, M. H. G. Wong, S. Qiu, Q. Sheng, X. Li, and Z. Song. 2015. Climate change-induced decline in bamboo habitats and species diversity: implications for giant panda conservation. Diversity and Distributions 21:379–391.

Lindsay, D. L., K. R. Barr, R. F. Lance, S. A. Tweddale, T. J. Hayden, and P. L. Leberg. 2008. Habitat fragmentation and genetic diversity of an endangered, migratory songbird, the golden-cheeked warbler (Dendroica chrysoparia). Molecular Ecology 17:2122–2133.

Littlefield, C. E., M. Krosby, J. L. Michalak, and J. J. Lawler. 2019. Connectivity for species on the move: supporting climate-driven range shifts. Frontiers in Ecology and the Environment 17:270–278.

Long, A. M., M. E. Marshall, M. L. Morrison, K. B. Hays, and S. L. Farrell. 2017. Responses of a Federally Endangered Songbird to Understory Thinning in Oak-Juniper Woodlands. Environmental Management 59:684–692.

Lurgi, M., B. W. Brook, F. Saltré, and D. A. Fordham. 2015. Modelling range dynamics under global change: which framework and why? Methods in Ecology and Evolution 6:247–256.

Magness, D. R., R. N. Wilkins, and S. J. Hejl. 2006. Quantitative Relationships Among Golden-Cheeked Warbler Occurrence and Landscape Size, Composition, and Structure. Wildlife Society Bulletin 34:473–479.

Marshall, M. E., M. L. Morrison, and R. N. Wilkins. 2013. Tree Species Composition and Food Availability Affect Productivity of an Endangered Species: The Golden-Cheeked Warbler. The Condor 115:882–892.

Mathewson, H. A., J. E. Groce, T. M. McFarland, M. L. Morrison, J. C. Newnam, R. T. Snelgrove, B. A. Collier, and R. N. Wilkins. 2012. Estimating breeding season abundance of golden-cheeked warblers in Texas, USA. The Journal of Wildlife Management 76:1117–1128.

McLaughlin, B. C., S. A. Skikne, E. Beller, R. V. Blakey, R. L. Olliff-Yang, N. Morueta-Holme, N. E. Heller, B. J. Brown, and E. S. Zavaleta. 2022. Conservation strategies for the climate crisis: An update on three decades of biodiversity management recommendations from science. Biological Conservation 268:109497.

Moore, G. W., C. B. Edgar, J. G. Vogel, R. A. Washington-Allen, R. G. March, and R. Zehnder. 2016. Tree mortality from an exceptional drought spanning mesic to semiarid ecoregions. Ecological Applications 26:602–611.

Moore, S. E., and H. P. Huntington. 2008. Arctic Marine Mammals and Climate Change: Impacts and Resilience. Ecological Applications 18:S157–S165.

Morelli, T. L., C. Daly, S. Z. Dobrowski, D. M. Dulen, J. L. Ebersole, S. T. Jackson, J. D. Lundquist, C. I. Millar, S. P. Maher, W. B. Monahan, K. R. Nydick, K. T. Redmond, S. C. Sawyer, S. Stock, and S. R. Beissinger. 2016. Managing Climate Change Refugia for Climate Adaptation. PLOS ONE 11:e0159909.

Morrison, M. L., R. N. Wilkins, B. A. Collier, J. E. Groce, H. A. Mathewson, T. M. McFarland, A. G. Snelgrove, R. T. Snelgrove, and K. L. Skow. 2010. Golden-cheeked warbler population distribution and abundance. Texas A&M Institute of Renewable Natural Resources, College Station, Texas, USA.

Mueller, J. M., S. E. Sesnie, S. E. Lehnen, H. T. Davis, J. J. Giocomo, J. N. Macey, and A. M. Long. 2022. Multi-scale species density model for conserving an endangered songbird. The Journal of Wildlife Management 86:e22236.

Nielsen-Gammon, J., S. Holman, A. Buley, S. Jorgensen, J. Escobedo, C. Ott, J. Dedrick, and A. Van Fleet. 2021. Assessment of Historic and Future Trends of Extreme Weather in Texas, 1900-2036: 2021 Update. Office of the State Climatologist, Texas A&M University, College Station:44.

O’Donnell, L., C. C. Farquhar, J. W. Hunt, K. Nesvacil, J. L. Reidy, W. Reiner Jr., J. L. Scalise, and C. C. Warren. 2019. Density influences accuracy of model-based estimates for a forest songbird. Journal of Field Ornithology 90:80–90.

O’Donnell, L., B. J. Pickles, C. M. Campbell, L. L. Moulton, N. M. Hauwert, and M. A. Gorzelak. 2020. Native tree and shrub canopy facilitates oak seedling regeneration in semiarid woodland. Ecosphere 11:e03017.

O’Neill, B. C., C. Tebaldi, D. P. van Vuuren, V. Eyring, P. Friedlingstein, G. Hurtt, R. Knutti, E. Kriegler, J.-F. Lamarque, J. Lowe, G. A. Meehl, R. Moss, K. Riahi, and B. M. Sanderson. 2016. The Scenario Model Intercomparison Project (ScenarioMIP) for CMIP6. Geoscientific Model Development 9:3461–3482.

Parding, K. M., A. Dobler, C. F. McSweeney, O. A. Landgren, R. Benestad, H. B. Erlandsen, A. Mezghani, H. Gregow, O. Räty, E. Viktor, J. El Zohbi, O. B. Christensen, and H. Loukos. 2020. GCMeval – An interactive tool for evaluation and selection of climate model ensembles. Climate Services 18:100167.

Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37–42.

Peak, R. G., and F. R. Thompson III. 2014. Seasonal productivity and nest survival of Golden-cheeked Warblers vary with forest type and edge density. The Condor 116:546–559.

Polley, H. W., D. M. Johnson, and R. B. Jackson. 2016. Canopy foliation and area as predictors of mortality risk from episodic drought for individual trees of Ashe juniper. Plant Ecology 217:1105–1114.

Polley, H. W., D. M. Johnson, and R. B. Jackson. 2018. Projected drought effects on the demography of Ashe juniper populations inferred from remote measurements of tree canopies. Plant Ecology 219:1259–1267.

Portalier, S. M. J., J.-N. Candau, and F. Lutscher. 2022. A temperature-driven model of phenological mismatch provides insights into the potential impacts of climate change on consumer–resource interactions. Ecography 2022:e06259.

Pulich, W. M. 1976. Review of The Golden-Cheeked Warbler. The Auk 94:799–801.

Reemts, C. M., and L. L. Hansen. 2008. Slow recolonization of burned oak–juniper woodlands by Ashe juniper (Juniperus ashei): Ten years of succession after crown fire. Forest Ecology and Management 255:1057–1066.

Reemts, C. M., C. Picinich, and J. H. Sperry. 2024. Crown fires remove a fire-sensitive canopy dominant from oak-juniper woodlands: results from long-term monitoring of wildfires. Fire Ecology 20:73.

Reidy, J. L., E. A. Sinnott, F. R. Thompson III, and L. O’Donnell. 2023. Urban land cover and El Niño events negatively impact population viability of an endangered North American songbird. Ecosphere 14:e4583.

Reidy, J. L., F. R. Thompson III, G. M. Connette, and L. O’Donnell. 2018. Demographic rates of Golden-cheeked Warblers in an urbanizing woodland preserve. The Condor 120:249–264.

Reidy, J. L., F. R. Thompson, and L. O’Donnell. 2020. Population Viability of Golden-cheeked Warblers in an Urbanizing Landscape. Wildlife Society Bulletin 44:502–511.

Reidy, J. L., F. R. Thompson, S. Rowin, C. Schwope, and J. M. Mueller. 2021. Effects of prescribed fire on fuels, vegetation, and Golden-cheeked warbler (*Setophaga chrysoparia*) demographics in

Texas juniper-oak woodlands: An update six years post-fire. Forest Ecology and Management 492:119191.

Román-Palacios, C., and J. J. Wiens. 2020. Recent responses to climate change reveal the drivers of species extinction and survival. Proceedings of the National Academy of Sciences of the United States of America 117:4211–4217.

Schumaker, N. H., and A. Brookes. 2018. HexSim: a modeling environment for ecology and conservation. Landscape ecology 33:197–211.

Schwantes, A. M., A. J. Parolari, J. J. Swenson, D. M. Johnson, J.-C. Domec, R. B. Jackson, N. Pelak, and A. Porporato. 2018. Accounting for landscape heterogeneity improves spatial predictions of tree vulnerability to drought. New Phytologist 220:132–146.

Schwantes, A. M., J. J. Swenson, M. González-Roglich, D. M. Johnson, J.-C. Domec, and R. B. Jackson. 2017. Measuring canopy loss and climatic thresholds from an extreme drought along a fivefold precipitation gradient across Texas. Global Change Biology 23:5120–5135.

Schwantes, A., J. Swenson, and R. Jackson. 2016. Quantifying drought-induced tree mortality in the open canopy woodlands of central Texas. Remote Sensing of Environment 181:54–64.

Sellar, A. A., C. G. Jones, J. P. Mulcahy, Y. Tang, A. Yool, A. Wiltshire, F. M. O'Connor, M. Stringer, R. Hill, J. Palmieri, S. Woodward, L. de Mora, T. Kuhlbrodt, S. T. Rumbold, D. I. Kelley, R. Ellis, C. E. Johnson, J. Walton, N. L. Abraham, M. B. Andrews, T. Andrews, A. T. Archibald, S. Berthou, E. Burke, E. Blockley, K. Carslaw, M. Dalvi, J. Edwards, G. A. Folberth, N. Gedney, P. T. Griffiths, A. B. Harper, M. A. Hendry, A. J. Hewitt, B. Johnson, A. Jones, C. D. Jones, J. Keeble, S. Liddicoat, O. Morgenstern, R. J. Parker, V. Predoi, E. Robertson, A. Siahaan, R. S. Smith, R. Swaminathan, M. T. Woodhouse, G. Zeng, and M. Zerroukat. 2019.

UKESM1: Description and Evaluation of the U.K. Earth System Model. Journal of Advances in Modeling Earth Systems 11:4513–4558.

Sesnie, S. E., J. M. Mueller, S. E. Lehnen, S. M. Rowin, J. L. Reidy, and F. R. Thompson III. 2016. Airborne laser altimetry and multispectral imagery for modeling Golden-cheeked Warbler (Setophaga chrysoparia) density. Ecosphere 7:e01220.

Stambaugh, M. C., G. Creacy, J. Sparks, and M. Rooney. 2017. Three centuries of fire and forest vegetation transitions preceding Texas' most destructive wildfire: Lost Pines or lost oaks? Forest Ecology and Management 396:91–101.

Stambaugh, M. C., J. C. Sparks, and E. R. Abadir. 2014. Historical Pyrogeography of Texas, USA. Fire Ecology 10:72–89.

U.S. Fish and Wildlife Service [USFWS]. 1990a. Endangered and threatened wildlife and plants—emergency rule to list the golden-cheeked warbler as endangered. Federal Register 55:18844–18845

U.S. Fish and Wildlife Service [USFWS]. 2025. Golden-cheeked warbler (*Setophaga chrysoparia*) 5-Year Review: Summary and Evaluation

Wilkening, J., W. Pearson-Prestera, N. A. Mungi, and S. Bhattacharyya. 2019. Endangered species management and climate change: When habitat conservation becomes a moving target. Wildlife Society Bulletin 43:11–20.

Yukimoto, S., H. Kawai, T. Koshiro, N. Oshima, K. Yoshida, S. Urakawa, H. Tsujino, M. Deushi, T. Tanaka, M. Hosaka, S. Yabu, H. Yoshimura, E. Shindo, R. Mizuta, A. Obata, Y. Adachi, and M. Ishii. 2019. The Meteorological Research Institute Earth System Model Version 2.0, MRI-ESM2.0: Description and Basic Evaluation of the Physical Component. Journal of the Meteorological Society of Japan. Ser. II 97:931–965.

CONCLUSION

Using a model-based approach, this research provides insight into the potential effects of climate-driven landscape change on the persistence of the Golden-cheeked Warbler (*Setophaga chrysoparia*). By integrating climate-driven projections of changes in the distribution of Ashe juniper—a key resource for the Golden-cheeked Warbler—with a recent habitat modeling effort, we generated a time series of habitat change upon which we modeled population dynamics of the warbler using a spatially explicit, individual-based, population model. The results suggest that climate-induced resource loss poses a substantial threat to warbler populations within its breeding range, painting a dire picture for this endangered species.

In chapter 1, I focused on understanding the implications of the warbler having an obligatory dependence on Ashe juniper (*Juniperus ashei*) for nest construction. Through a species distribution model, we observed a stark decline in suitable conditions for Ashe juniper, with projections ranging from a 70% range reduction under a moderate emission scenario to a near-complete loss (99%) by 2100 under the most extreme scenarios. This projected suitability loss serves as a warning, highlighting the vulnerability of a necessary resource for the warbler and raising concerns about the warbler's long-term viability.

Building on this foundation, in chapter 2, I used a population model to explore the cascading effects of this resource loss on warbler populations. By integrating the SDM projections into my spatially explicit population model, I simulated warbler occupancy under four climate futures (Schumaker and Brookes 2018). The results mirrored the trends observed in the SDM, with substantial declines in warbler populations across all scenarios. These declines were particularly extensive under the most extreme climate projections from the UKESM1-0-LL generalized circulation model. While the average of the SSP2-4.5 scenarios suggests a population decline of approximately 52% by 2090, the resulting potentially stable population may not actually be established if climate mitigation and habitat protection strategies are not implemented. Most importantly, this chapter identified potential refugia on actively managed lands (e.g., Balcones Canyonlands Preserve, Balcones Canyonlands National Wildlife Refuge, Fort Cavazos), offering consistent spatial targets for conservation efforts.

Although both chapters hold inherent uncertainties in the modeling approaches, the results converge on a central message. It is clear that climate change poses a severe threat to Golden-cheeked Warbler populations. Although my models suggest the potential for population stabilization under certain conditions, the magnitude of the projected declines emphasizes the urgent need for proactive conservation interventions, especially within the identified refugia. Furthermore, I highlight the need for future research to incorporate additional stressors, such as urbanization, drought, fire and their interactive effects on warbler demographics, to provide a more holistic understanding of the warbler’s vulnerability to extinction.