Ornithological Applications, 2024, 126, 1–18
https://doi.org/10.1093/ornithapp/duae032
Advance access publication 23 July 2024
Research Article

Ornithological Applications
OXFORD

Nonbreeding distributions of four declining Nearctic–Neotropical migrants are predicted to contract under future climate and socioeconomic scenarios

Ryan E. Brodie,[1,2,*] Nicholas J. Bayly,[3,‡] Ana M. González,[4,‡] Jessica Hightower,[5,‡] Jeffery L. Larkin,[6,7,‡] Rebecca L. M. Stewart,[8,‡] Scott Wilson,[9,10,‡] and Amber M. Roth[1,2,‡]

[1]School of Forest Resources, University of Maine, Orono, Maine, USA
[2]Department of Wildlife, Fisheries, and Conservation Biology, University of Maine, Orono, Maine, USA
[3]SELVA Investigación para la Conservación en el Neotropico, Bogotá, Colombia
[4]Canadian Wildlife Service, Environment and Climate Change Canada, Delta, British Columbia, Canada
[5]Department of Forest Ecosystems and Society, Oregon State University, Corvallis, Oregon, USA
[6]Department of Biology, Indiana University of Pennsylvania, Indiana, Pennsylvania, USA
[7]American Bird Conservancy, The Plains, Virginia, USA
[8]Canadian Wildlife Service, Environment and Climate Change Canada, Gatineau, Quebec, Canada
[9]Department of Forest and Conservation Sciences, University of British Columbia, Vancouver, British Columbia, Canada
[10]Wildlife Research Division, Environment and Climate Change Canada, Delta, British Columbia, Canada

[*]Corresponding author: ryan.brodie@maine.edu
[‡]These authors contributed equally to the paper.

ABSTRACT

Climate and land use/land cover change are expected to influence the stationary nonbreeding distributions of 4 Nearctic–Neotropical migrant bird species experiencing population declines: *Cardellina canadensis* (Canada Warbler), *Setophaga cerulea* (Cerulean Warbler), *Vermivora chrysoptera* (Golden-winged Warbler), and *Hylocichla mustelina* (Wood Thrush). Understanding how and where these species' distributions shift in response to environmental drivers is critical to inform conservation planning in the Neotropics. For each species, we quantified current (2012 to 2021) and projected future (2050) suitable climatic and land use/land cover conditions as components of stationary nonbreeding distributions. Multi-source occurrence data were used in an ensemble modeling approach with covariates from 3 global coupled climate models (CMCC-ESM2, FIO-ESM-2-0, MIROC-ES2L) and 2 shared socioeconomic pathways (SSP2-RCP4.5, SSP5-RCP8.5) to predict distributions in response to varying climatic and land use/land cover conditions. Our findings suggest that distribution contraction, upslope elevational shifts in suitable conditions, and limited shifts in latitude and longitude will occur in 3 of 4 species. *Cardellina canadensis* and *S. cerulea* are expected to experience a moderate distribution contraction (7% to 29% and 19% to 43%, respectively), primarily in response to expected temperature changes. The *V. chrysoptera* distribution was modeled by sex, and females and males were projected to experience a major distribution contraction (56% to 79% loss in suitable conditions for females, 46% to 65% for males), accompanied by shifts in peak densities to higher elevations with minimal changes in the upper elevation limit. Expected changes in precipitation had the greatest effect on *V. chrysoptera*. *Hylocichla mustelina* experienced the smallest distribution change, consistent with the species' flexibility in habitat selection and broader elevational range. We recommend defining priority areas for conservation as those where suitable conditions are expected to remain or arise in the next 25 years. For *V. chrysoptera* in particular, it is urgent to ensure that mid-elevation forests in Costa Rica and Honduras are adequately managed and protected.

Keywords: climate change, conservation planning, distribution contraction, focal areas, land cover change, land use change, migratory birds, Neotropics

How to Cite

Brodie, R. E., N. J. Bayly, A. M. González, J. Hightower, J. L. Larkin, R. L. M. Stewart, S. Wilson, and A. M. Roth (2024). Nonbreeding distributions of four declining Nearctic–Neotropical migrants are predicted to contract under future climate and socioeconomic scenarios. Ornithological Applications 126:duae032.

LAY SUMMARY

- We predicted nonbreeding distribution changes between current (2012 to 2021) and future (2050) timeframes for 4 at-risk migratory landbirds wintering in the Neotropics.
- The distribution of each species is predicted to notably contract and shift minimally in latitude and longitude.
- *Cardellina canadensis* (Canada Warbler) and *Setophaga cerulea* (Cerulean Warbler) occupy similar habitats in northern South America and respond to climate and land use/land cover change by shifting upslope in elevation.
- Precipitation patterns had the greatest influence on the distribution of *Vermivora chrysoptera* (Golden-winged Warbler), and distribution contraction was most severe for this species.

Submission Date: March 3, 2024. Editorial Acceptance Date: June 26, 2024

- *Hylocichla mustelina* (Wood Thrush) is predicted to be the least affected of the 4 species studied by changing environments.
- Methods used in this study can improve identification and prioritization of protected and conserved areas in the near-term that can be applied to conservation planning.

Se reducirá la distribución no reproductiva de cuatro especies de aves migratorias Neártico-Neotropicales en declive bajo futuros escenarios climáticos y socioeconómicos

RESUMEN

Se espera que el cambio climático y los cambios en el uso/cobertura del suelo influyen en la distribución no-reproductiva de cuatro especies de aves migratorias neártico-neotropicales en declive: *Cardellina canadensis*, *Setophaga cerulea*, *Vermivora chrysoptera* y *Hylocichla mustelina*. Comprender cómo y dónde cambian las distribuciones de estas especies en respuesta a los factores detonantes ambientales es fundamental para informar a los procesos de conservación en el Neotrópico. Para cada especie, cuantificamos las condiciones climáticas y las coberturas del suelo óptimas para el periodo actual (2012 a 2021) y para el futuro (2050), como componentes de la distribución no reproductiva estacionaria. Al juntar datos de múltiples fuentes sobre la presencia de aves, utilizamos el método de modelos de conjuntos con covariables de tres modelos climáticos globales (CMCC-EMS2, FIO-ESM-2-0, MIROC-ES2L) y dos trayectorias socioeconómicas compartidas (SSP2-RCP4.5, SSP5-RCP8.5) para predecir la distribución de las aves en respuesta a diferentes condiciones climáticas y de uso del suelo. Nuestros hallazgos sugieren que 3 de las 4 especies estudiadas experimentarán una contracción en su distribución, acompañada por un desplazamiento en las condiciones óptimas hacia elevaciones mayores y cambios limitados en latitud y longitud. Se encontró que *C. canadensis* y *S. cerulea* sufrirán una contracción moderada de distribución (7 al 29% y 19 al 43%, respectivamente) en respuesta a los cambios esperados, principalmente por aumentos en temperatura. La distribución no-reproductiva de *V. chrysoptera* se modeló por sexo, y se proyectó que las hembras (♀) y los machos (♂) experimentarán una fuerte contracción de distribución (una reducción de 56 al 79% en las condiciones aptas para ♀ y de 46 al 65% para ♂), acompañado por aumentos en abundancia a elevaciones mayores, pero con un cambio mínimo en el límite de elevación superior. Los cambios esperados en los patrones de precipitación tuvieron el mayor efecto en *V. chrysoptera*. Los cambios esperados en *H. mustelina* fueron menores, lo cual es consistente con su flexibilidad ante la selección de hábitat y su uso de un amplio rango de elevaciones. Recomendamos definir áreas prioritarias para la conservación como aquellas donde se espera que las condiciones óptimas se mantengan o aparecerán en los próximos 25 años. Para *V. chrysoptera*, en particular, es urgente asegurar la gestión y protección adecuada para los bosques a elevaciones medias en Costa Rica y Honduras.

Palabras clave: áreas focales, aves migratorias, cambio climático, cambio de uso del suelo, cambio en la cobertura del suelo, contracción de la distribución, Neotrópico, planes de conservación

INTRODUCTION

Many Nearctic–Neotropical (hereinafter, Neotropical) migrant birds are undergoing steep population declines (Rosenberg et al. 2019) with climate and land use/land cover (hereinafter, LULC) changes on the stationary nonbreeding grounds identified as a likely cause for several species (González-Prieto et al. 2017, Kramer et al. 2017, Wilson et al. 2018, Céspedes Arias et al. 2022). Endeavors to reverse declines will be aided by an understanding of the factors influencing distributions, and how distributions are likely to be impacted by future climate and LULC changes in nonbreeding regions. Historically, most research on this topic has focused on breeding regions (Marra et al. 2015, Soares et al. 2023), meaning we lack this information for most species during the nonbreeding period. Determining responses of declining Neotropical migrants to climate and LULC driven shifts will therefore aid our understanding of full-annual cycle dynamics and inform conservation planning efforts for migratory birds on the nonbreeding grounds.

Conservation strategies may be more adaptive if projections of species responses to future climate and LULC change are included (Whitney et al. 2023). However, conservation areas are generally identified and prioritized based on current information on species locations, habitat selection, and other factors (e.g., habitat degradation) rather than information on projected species distributions (Groves et al. 2012, Whitney et al. 2023). Projected distributions can be used to connect conservation areas through space and time to accommodate shifts, and to develop a suite of possible outcomes in current and future environments (Groves et al. 2012, Bax et al. 2021). The inclusion of projections in conservation strategies can help direct finite resources to areas where they can be most effective, both under current conditions and in the near-term (i.e., in the next 25 years).

Neotropical migrants exhibit strong affiliations to precipitation regimes in stationary nonbreeding regions (Bennett et al. 2019, Stanley et al. 2021, Céspedes Arias et al. 2022), making them vulnerable to increasing temperatures and precipitation seasonality (Fuentes-Franco et al. 2014, Almazroui et al. 2021). Previous studies have found evidence for elevational shifts in species distributions due to climate change for tropical resident bird species (Freeman et al. 2018) and migratory species on temperate breeding grounds (Maggini et al. 2011, Tingley et al. 2012, Hightower et al. 2023). However, to our knowledge, no previous studies have considered how climate change will impact elevation ranges for Neotropical migrants on their tropical stationary nonbreeding grounds. Of particular concern is the "escalator to extinction," which describes an expected shift of a species' distribution to higher elevations, with a fixed upper elevational limit but little latitudinal movement (Sekercioglu et al. 2008, Freeman et al. 2018). Restricted space and resources may advance climatic pressures on bird species if limiting factors, such as vulnerability to habitat fragmentation (Gómez et al. 2015) or limited areal extents of habitat (Freeman et al. 2018), are more severe at higher elevations. Further, habitat fragmentation is a contributing factor to population declines among Neotropical migrants (Colorado et al. 2012, González-Prieto et al. 2017, Wilson et al. 2018, Roth et al. 2019) and may impact the functional diversity of Neotropical bird communities (Fontúrbel et al. 2022, Mariano-Neto and Santos 2023), making conservation planning more important now than ever before.

Resources and capacity for forest and agroforestry conservation are limited in the Neotropics (Wilson et al. 2022, González et al. 2023b). Conservation Investment Strategies (hereinafter, CISs) prioritize conservation through an economic lens and are intended to improve the allocation of finite resources to areas where they can be most effective in reversing the decline of imperiled species (Wilson et al. 2022, González et al. 2023b). In this study, we focused on 4 at-risk forest bird species experiencing steep population declines, and which are the conservation targets of 3 CISs in Central and South America (Morales et al. 2022, Sánchez-Nivicela and Montenegro-Pazmiño 2022, González et al. 2023a): *Cardellina canadensis* (Canada Warbler, CAWA), *Setophaga cerulea* (Cerulean Warbler, CERW), *Vermivora chrysoptera* (Golden-winged Warbler, GWWA), and *Hylocichla mustelina* (Wood Thrush, WOTH). Given these species' habitat preferences for forest and agroforestry (e.g., shade-coffee) habitats at low- and mid-elevations (Buehler et al. 2020, Confer et al. 2020, Evans et al. 2020, Reitsma et al. 2020), it is reasonable to postulate that their recovery will be influenced by climatic and LULC pressures over the next several decades.

The goal of this research was to identify the environmental factors influencing the distributions of the 4 focal bird species and predict how those distributions will be impacted by future climate and LULC change to inform conservation planning. Specifically, we sought to understand the effects of climate and LULC change on the stationary nonbreeding distributions of the focal species by mapping current (2012 to 2021) and future (2050) suitable climatic and LULC conditions as components of the distributions. Two shared socioeconomic pathways (SSP-RCP) and 3 global coupled climate models (GCCM) were used in an ensemble model approach (Thuiller et al. 2009, Hightower et al. 2023). From current and future suitable conditions, we first identified predicted shifts in elevation, latitude, and longitude, along with climatic and LULC covariates driving distribution shifts for the focal species. Second, to facilitate the identification of high-priority conservation areas, we modeled occupied current ranges and overlapped them with our predictions of current suitable climatic and LULC conditions. This analysis helped us identify locations with suitable conditions that the focal species inhabit, provided insights for where the focal species may occupy landscapes with unsuitable conditions, and where suitable conditions elsewhere may permit colonization in the near-term. Third, to illustrate how this combination approach can assist conservation planning, we compared and contrasted our results for *V. chrysoptera* and focal areas in Honduras delineated for the *V. chrysoptera* nonbreeding season conservation plan (Bennett et al. 2016).

METHODS

Focal Bird Species

Cardellina canadensis (between 1,000 and 2,200 m elevation) and *S. cerulea* (between 500 and 2,000 m elevation) inhabit mid-elevation forests and shade-coffee agriculture in the Andes of northwestern South America (Céspedes Arias et al. 2022). *Vermivora chrysoptera* prefers mid-elevation forests with semi-open canopies and forest edges <2,500 m elevation in Central America and northwestern South America (Roth et al. 2019). Importantly, the species exhibits habitat segregation by sex (Bennett et al. 2019). *Hylocichla mustelina* inhabits many closed-canopy forests between 50 and 1,000 m elevation in Central America and southern Mexico (Evans et al. 2020). The species uses shade-coffee agriculture as secondary habitat despite notable mortality in those environments at higher elevations (Bailey and King 2019).

Bird Occurrence Data

We obtained current (2012 to 2021) bird occurrence data containing only Neotropical presence records from eBird (accessed in January 2023; Sullivan et al. 2009) and supplemented with species-specific georeferenced occurrence datasets (Supplementary Table 1) to bolster presence record sample sizes and the spatial representation of records. 2012 to 2021 was identified as the "current" timeframe to capitalize on increased user engagement with eBird and align with prior research (Hightower et al. 2023). Date ranges for the stationary nonbreeding period were defined using expert input (N. Bayly, E. Cohen, I. Davidson, A. González, J. Hightower, J. L. Larkin, E. Montenegro, D. Raybuck, A. Roth, C. Rushing, C. Stanley, R. L. M. Stewart, and S. Wilson personal communication) to assess frequency distributions of daily presence records in the current timeframe. Experts emphasized date selection 2 weeks before or after most birds initiated or completed migration through the Neotropical flyway to minimize the signal from areas used during migration (*C. canadensis*: November 16 to March 17, *S. cerulea*: October 25 to March 10, *V. chrysoptera*: October 28 to March 31, *H. mustelina*: November 5 to March 28).

eBird occurrence data were filtered in R with the *auk* package (Strimas-Mackey et al. 2018, R Core Team 2022) to select presence records collected using "traveling," "stationary," and "incidental" protocols with observer effort distances ≤2 km (Medina et al. 2023). Duplicate records, as well as outlier records from areas outside of known stationary nonbreeding locations (Fink et al. 2022), were removed. We added the species-specific datasets to filtered eBird datasets and resampled all presence records to a 1-km^2 resolution (Fick and Hijmans 2017). The final dataset included 5,765 unique presence records for the current timeframe (*C. canadensis*: $n = 1,586$, *S. cerulea*: $n = 546$, *V. chrysoptera* ♀: $n = 192$, *V. chrysoptera* ♂: $n = 283$, *H. mustelina*: $n = 3,158$). We partitioned *V. chrysoptera* records by sex as it is a sexually dimorphic species allowing for possible identification by plumage. The sexes are known to segregate by habitat and elevation resulting in conservation planning bias in favor of higher elevations for males (Bennett et al. 2019). Thus, we removed records that did not specify sex ($n = 1,860$).

Climate and Land Use/Land Cover Data

We downloaded historical (1970 to 2000 averages) monthly climatic and bioclimatic raster datasets at a 30-arc second (~1-km^2) spatial resolution from the WorldClim data repository (Fick and Hijmans 2017). Historical climate data aided predictions of current climatic and LULC conditions with documented ecological patterns (Acevedo et al. 2012). Bioclimatic covariates were selected based on literature review, expert input, principal component analysis (PCA) correlation circles, and predictor contribution percentages. PCA correlation circles and predictor contribution percentages were used to identify multicollinearities among bioclimatic covariates (Fick and Hijmans 2017, Guisan et al. 2017). We selected bioclimatic covariates for ensemble modeling (Thuiller et al. 2009, Guisan et al. 2017) that were above the expected average contribution percentage, a product of

TABLE 1. List of climatic (CMIP6; Fick and Hijmans 2017), topographic (Fick and Hijmans 2017, Esri Inc. 2022), and plant functional types (Chen et al. 2022) datasets used as covariates for ensemble modeling and projected suitable climatic and LULC conditions. Species abbreviations: *Cardellina canadensis* (Canada Warbler, CAWA), *Setophaga cerulea* (Cerulean Warbler, CERW), *Vermivora chrysoptera* (Golden-winged Warbler, GWWA), and *Hylocichla mustelina* (Wood Thrush, WOTH).

Variable	Description	Species
BIO1	Annual Mean Temp	CAWA, CERW, GWWA, WOTH
BIO2	Mean Diurnal Range	WOTH
BIO3	Isothermality	WOTH
BIO4	Temp Seasonality	WOTH
BIO5	Max Temp of Warmest Month	CAWA, CERW, GWWA
BIO6	Min Temp of Coldest Month	CAWA, CERW, GWWA, WOTH
BIO7	Temp Annual Range	GWWA, WOTH
BIO8	Mean Temp of Wettest Quarter	CAWA, CERW, GWWA
BIO9	Mean Temp of Driest Quarter	CAWA, CERW, GWWA
BIO10	Mean Temp of Warmest Quarter	CAWA, CERW, GWWA
BIO11	Mean Temp of Coldest Quarter	CAWA, CERW, GWWA, WOTH
BIO12	Annual Precip	CAWA, CERW, GWWA, WOTH
BIO13	Precip of Wettest Month	WOTH
BIO14	Precip of Driest Month	CAWA, CERW, WOTH
BIO15	Precip Seasonality	CAWA, CERW, WOTH
BIO16	Precip of Wettest Quarter	GWWA, WOTH
BIO17	Precip of Driest Quarter	CAWA, CERW, WOTH
BIO19	Precip of Coldest Quarter	WOTH
Precip01	Total Precip of January	CAWA, CERW, GWWA, WOTH
Precip02	Total Precip of February	CAWA, CERW, GWWA, WOTH
Precip03	Total Precip of March	CAWA, CERW, GWWA, WOTH
Precip10	Total Precip of October	CERW, GWWA
Precip11	Total Precip of November	CAWA, CERW, GWWA, WOTH
Precip12	Total Precip of December	CAWA, CERW, GWWA, WOTH
TMin03	Avg Min Temp of March	CAWA, CERW, GWWA, WOTH
TMin10	Avg Min Temp of October	CERW, GWWA
TMin11	Avg Min Temp of November	CAWA, WOTH
TMax03	Avg Max Temp of March	CAWA, CERW, GWWA, WOTH
TMax10	Avg Max Temp of October	CERW, GWWA
TMax11	Avg Max Temp of November	CAWA, WOTH
Elevation	Digital Elevation Model (DEM)	CAWA, CERW, GWWA, WOTH
Slope	Derived from DEM	CAWA, CERW, GWWA, WOTH
PFT	Plant Functional Types	CAWA, CERW, GWWA, WOTH

the covariate eigenvalues (Dray et al. 2023). Further, elevation and slope were derived from an $\sim$1-km^2 digital elevation model (Fick and Hijmans 2017) in ArcGIS Pro 3.0.0 (Esri Inc. 2022). Global LULC projections based on simulations of 16 plant functional types (i.e., forest, grassland, and cropland) and urban expansion (see figure 2 in Chen et al. 2022) were included to simulate effects of LULC change. We used the resulting covariates in ensemble modeling to capture species responses from the current timeframe based on historical climate (*C. canadensis*: $n = 23$ covariates, *S. cerulea*: $n = 24$, ♀ *V. chrysoptera*: $n = 23$, ♂ *V. chrysoptera*: $n = 23$, *H. mustelina*: $n = 26$) (Table 1).

For future (2050) climatic and LULC conditions, we obtained climatic datasets (2041 to 2060 averages) identical to the historical dataset from WorldClim for 3 individual GCCMs: the CMCC-ESM2 (Cherchi et al. 2019), the FIO-ESM-2-0 (Bao et al. 2020), and the MIROC-ES2L (Hajima et al. 2020). For each GCCM, we used 2 2041 to 2060 SSP-RCP scenarios which represent independent climatic futures: SSP2-RCP4.5 and SSP5-RCP8.5 (Fick and Hijmans 2017). SSP2-RCP4.5 (hereinafter, best-case) represents a future where climate-smart practices increase and nonrenewable resource use declines (Van Vuuren et al. 2011, Riahi et al. 2017). In contrast, SSP5-RCP8.5 (hereinafter, worst-case) represents a future where technological advances and increased fossil fuel extraction lead to maximum global emissions (Van Vuuren et al. 2011, Riahi et al. 2017).

The spatial extent used to extract climate and LULC data was identical among scenarios to project current species responses onto future climates (Guisan et al. 2017, Hightower et al. 2023). To accommodate potential distribution shifts in latitude and longitude by 2050, we initially included areas in the periphery of current stationary nonbreeding locations (Fink et al. 2022) for the spatial extents of each focal species. Preliminary analyses resulted in extralimital projections of species occurrence when suitable climatic and LULC conditions occurred well outside the current distribution of each species. To limit these projections, we defined the northern and southern termini of each spatial extent with a combination of the unique presence records and known current stationary nonbreeding locations (Fink et al. 2022). We applied a spatial constraint that prevented extralimital projections of occurrence that exceeded 200 km from known occurrences, but we filled gaps in presence record coverage where species are known to occupy (Fink et al. 2022). The 200-km distance was selected to accommodate reasonable dispersal distances for each species in the current timeframe (Barbet-Massin et al. 2012, Freeman et al. 2018).

Ensemble Modeling and Projected Distributions

We used an ensemble modeling framework within the R package *biomod2* (Thuiller et al. 2009, Guisan et al. 2017) to model current and future projections of suitable climatic and LULC conditions for the 4 focal bird species (*V. chrysoptera* ♀ and ♂ separately). To address multicollinearity and biases in ecological studies (Fotheringham and Oshan 2016), we incorporated 4 successful modeling algorithms (Qiao et al. 2015, Guisan et al. 2017): generalized linear model (GLM), generalized boosting model (GBM), generalized additive model (GAM), and random forest (RF). Default settings in *biomod2* were kept for GBM and RF, while settings were modified for GLM and GAM: We set the relationship between presence records and covariates to a polynomial function for GLM (Hightower et al. 2023), while the GAM modeling function was set to *GAM_mgcv* (Wood 2017).

Predictive performance of individual models

For each modeling algorithm plus 1 full model (models that are calibrated and validated over an entire pseudo-absence dataset), we used 5K-fold cross-validations with 70% and 30% of the occurrence records allocated for training and validations, respectively (Guisan et al. 2017). We evaluated modeling algorithm performances using TSS and receiver operating characteristic (ROC) metrics, where TSS values > 0.6 are good and ROC values > 0.9 are excellent (Thuiller et al. 2009, Guisan et al. 2017) (Supplementary Table 2).

We randomly generated pseudo-absence points in the modeling framework due to limited true-absence records in the Neotropics during the current timeframe. The number of pseudo-absences and presence records were roughly equal to aid in decision tree dynamics for GBM and RF (Barbet-Massin et al. 2012). Pseudo-absences were generated within a radius of 200-km from presence records, but no pseudo-absences were generated within the same 30 arc-second (~1 km^2) pixel of a presence record (Hightower et al. 2023). The maximum radius of 200-km permitted the modeling algorithms to train in different climatic and LULC conditions within reasonable dispersal distances in the Neotropics (Barbet-Massin et al. 2012, Freeman et al. 2018).

Including our unique presence records, 3 pseudo-absence runs were completed for 4 modeling algorithms, 5 model runs (i.e., cross-validations), 7 distributions (i.e., 1 current + 3 GCCMs × 2 SSP-RCPs), and 4 species (with *V. chrysoptera* ♀ and ♂ modeled separately) for an analysis of 2,100 individual models. Individual models with ROC scores > 0.9 and TSS scores > 0.6 were included in calculations for the ensemble models to augment sensitivity (i.e., predicted presences) and specificity (i.e., predicted absences) scores (Araújo and New 2007, Thuiller et al. 2009). We did not consider erroneous models that reached iteration limits without full convergence. The removal of low-scoring (80) and erroneous (3) models ensured that ensemble models were calculated with the best projections (i.e., 2,017 individual models). Committee-averaged ensemble model outputs were selected for post-processing analyses which represented consensus and disagreement among individual models (Araújo and New 2007, Guisan et al. 2017).

Covariate Evaluation

We identified the top 4 performing covariates by calculating mean covariate importance values from the GLM, GBM, GAM, and RF modeling algorithms (Hightower et al. 2023). The analysis of 4 covariates captured variety for each species and each modeling algorithm in a succinct manner. Importance values were interpreted within each modeling algorithm only. However, for each focal bird species, recurring covariates among modeling algorithms were noted to accommodate for predictive variance and identify the most influential environmental factors for committee-averaged ensemble model outputs (Bucklin et al. 2015). See Supplementary Material for details on spatial autocorrelation (Supplementary Figure 1) and caveats for our modeling framework.

Distribution Shifts Due to Changes in Suitable Conditions

We completed post-processing analyses in ArcGIS Pro 3.0.0 to assess conditions of suitable climatic and LULC conditions in current and future scenarios for each focal species. Pixel values < 0.5 in the committee-averaged ensemble model outputs were labeled as absences and were removed prior to analysis (Brown and Yoder 2015). We developed spatial products from the binary grids for suitable conditions lost, gained, and remaining between the current and future scenarios, where current suitable conditions were the reference for future suitable conditions (Hightower et al. 2023). Among the GCCMs used in this study, MIROC-ES2L (Hajima et al. 2020) was the most reported in the literature. Thus, the SSP2-RCP4.5 (best-case) MIROC-ES2L future scenario was used in the main text to highlight suitable conditions lost, remained, and gained for each focal species.

Histograms corresponding to elevation, latitude, and longitude were created to describe shifts in spatial patterns for the focal species (Da Silveira et al. 2021). We used the current and future binary grids as raster masks to determine elevation ranges in ArcGIS Pro 3.0.0, which were defined by the absolute minimum and maximum elevation values among the raster masks for each species. This standardization procedure allowed us to compare pixel counts at exact elevation values within the masked areas and among current and future scenarios, where histogram values were synonymous with available suitable conditions (Da Silveira et al. 2021). Latitudinal and longitudinal histograms were developed with similar methods as the elevation histograms, except that we extracted coordinates directly from the masked elevation rasters in R.

Comparison of Predicted Occupied Current Ranges to Predicted Current Suitable Conditions

We sought to compare predicted occupied current ranges to our predicted current suitable conditions (as components of stationary nonbreeding distributions) to facilitate the identification of high-priority conservation areas. To define the occupied current ranges for the focal species, we used high-resolution (~3-km^2) weekly abundance raster datasets from the *ebirdst* R package (Strimas-Mackey et al. 2023). Weekly abundance rasters for the focal species were selected according to the date ranges described above. We combined and resampled rasters to match the projected coordinate system and resolution of the binary grids developed previously. To minimize the influence of outliers and create a standardized raster layer, data within the 99th quantile were converted to values between 0 and 1 and any value < 0.01 was set to "NA" (Gómez and Flores 2023).

Having created a raster for the occupied current range, we compared it with the predicted current suitable conditions from the ensemble model in ArcGIS Pro 3.0.0 (Botero-Delgadillo et al. 2022). Abundance values < 0.1 were removed prior to analysis to ensure comparisons between the predictive methods were not overly restrictive but made without consideration of low probability use areas (Wilson et al. 2022). We developed 3 spatial layers for each species: (1) predicted current suitable conditions but currently unoccupied, (2) predicted current suitable conditions that are currently occupied, and (3) predicted current unsuitable conditions but currently occupied. Corresponding area totals were calculated as follows: (1) current suitable conditions—intersect between predictive methods, (2) intersect between predictive methods, and (3) occupied current range—intersect between predictive methods. The inclusion of probable occupied current ranges improved our confidence in developing a conceptual process to identify near-term conservation priority areas (Botero-Delgadillo et al. 2022).

Processes to Identify Near-term Conservation Priority Areas

Honduran focal areas were previously delineated for the *V. chrysoptera* nonbreeding season conservation plan (Bennett et al. 2016). For *V. chrysoptera* ♀ and ♂, we first intersected the "predicted current suitable conditions that are currently occupied" products with individual Honduran focal areas. Then, we merged suitable conditions remained and gained among each best-case future projection to capture spatial overlap in the near-term, and intersected those products with individual Honduran focal areas. Within individual focal areas, intersected area (km^2) and percent decline (from future intersected area/current intersected area) were calculated to assess the current and future validity of each boundary. We extended the mapping portion beyond Honduran focal area boundaries to consider areas for conservation expansion, where locations that satisfied the current and/or future spatial intersection could infer opportunities for resource allocation. Thereupon, we developed a conceptual process to identify near-term conservation priority areas, dependent on the preference of a conservation practitioner to maintain suitable landscapes within currently delineated conservation focal areas or to shift conservation action to areas that are likely to be suitable in the future (Groves et al. 2012, Bax et al. 2021).

RESULTS

Covariate Evaluation

Monthly and bioclimatic temperature covariates were the most influential among modeling algorithms, except for *V. chrysoptera* ♀ GBM/RF and *V. chrysoptera* ♂ GBM (Table 2), where precipitation covariates were more important. Slope was not considered a top-4 covariate among modeling algorithms, while elevation was included twice, and plant functional types (PFT) was included once for *H. mustelina* GBM.

Change in Area of Suitable Conditions

Contraction of suitable climatic and land use/land cover conditions

The total area of future suitable climatic and LULC conditions decreased from the current timeframe to 2050 for all focal species. The nonbreeding distribution of *C. canadensis* was projected to contract by 7% to 20%, whereas the *S. cerulea* distribution was projected to contract by 19% to 36% (Table 3). *Vermivora chrysoptera* ♀ and ♂ were projected to experience extensive distribution contractions of 46% to 75% under best-case future scenarios, highlighted by a strong negative response in the FIO-ESM-2-0 GCCM for ♀ (75%, Table 3). *Hylocichla mustelina* is expected to retain > 80% of its current suitable conditions in each future scenario. Among all focal species, the MIROC-ES2L GCCM projected the least amount of contraction. Note that percent change calculations were based on total area (km^2) alone and did not incorporate spatial intersections. See Supplementary Table 3 for worst-case spatial statistics.

Upslope elevational shifts

The upper elevation limit for suitable climatic and LULC conditions in future scenarios changed little for all focal species, but the lower elevation limit moved upslope for *C. canadensis*, *S. cerulea*, and *V. chrysoptera* ♀ (Figure 1A to C). Suitable conditions for *C. canadensis* and *S. cerulea* shifted 250 m at the lower elevational limit, whereas peak densities were projected to shift 500 m upslope. For *V. chrysoptera* ♀, suitable conditions were projected to be absent between sea level and 500 m elevation, with peak density shifting from 750 to 1,150 m. In comparison, suitable conditions for *V. chrysoptera* ♂ were projected to be maintained in low density at lower elevations, and peak density was projected to shift from 900 to 1,500 m (Figure 1D). The elevational range for *H. mustelina* suitable conditions was projected to remain similar under the future climatic and LULC scenarios (Figure 1E). Availability of suitable conditions by elevation for all species under the worst-case climate scenarios tracked closely to the best-case scenarios.

Distribution changes in latitude and longitude

Latitudinal and longitudinal shifts for availability of suitable conditions were limited. *Cardellina canadensis* density shifted little, resulting in a 40 km SSE change in the centroid coordinate location on average (Supplementary Table 4). For *S. cerulea*, latitudinal density increased from the equator to central Colombia (~7° north) with the centroid coordinate moving 72 km WNW on average (Supplementary Table 4 and Figure 2b). *Vermivora chrysoptera* ♀ peak longitudinal density shifted eastward from Honduras and western Nicaragua (~86° west) to Costa Rica (~84° west) with the centroid coordinate changing by 92 km SSW on average (Supplementary Table 4 and Figure 3c). Unlike *V. chrysoptera* ♀, ♂ peak longitudinal density increased in central and western Colombia (~74° west) among all future climate scenarios with the centroid coordinate shifting by 154 km SE on average (Supplementary Table 4 and Figure 3d). *Hylocichla mustelina* is projected to experience a 77-km SE centroid coordinate shift with little

TABLE 2. Top 4 covariates with highest importance values from the 4 modeling algorithms for each focal bird species. IVs should only be interpreted within each modeling algorithm. The most recurring covariate(s) within a species across all models is highlighted in **bold**. Species abbreviations: *Cardellina canadensis* (Canada Warbler, CAWA), *Setophaga cerulea* (Cerulean Warbler, CERW), *Vermivora chrysoptera* (Golden-winged Warbler, GWWA), and *Hylocichla mustelina* (Wood Thrush, WOTH).

	GLM		GBM		GAM		RF	
Species	Covariate	IV	Covariate	IV	Covariate	IV	Covariate	IV
CAWA	TMin11	0.95	**TMax11**	0.073	TMin11	0.99	**TMax11**	0.058
	TMax11	0.63	**BIO8**	0.042	BIO1	0.99	**BIO8**	0.042
	BIO11	0.59	BIO5	0.033	BIO11	0.58	BIO5	0.040
	BIO8	0.54	BIO17	0.023	TMin03	0.46	Elevation	0.037
CERW	**BIO5**	0.86	**BIO5**	0.12	**BIO5**	0.95	**BIO5**	0.047
	TMin10	0.61	BIO8	0.071	TMin10	0.83	BIO17	0.034
	TMax10	0.33	Precip11	0.043	BIO11	0.70	BIO8	0.031
	BIO10	0.26	BIO17	0.036	BIO1	0.59	TMax10	0.020
GWWA ♀	**TMin10**	0.52	**Precip03**	0.061	**BIO7**	0.97	**Precip03**	0.021
	BIO5	0.49	**Precip11**	0.052	BIO6	0.94	**Precip11**	0.017
	Elevation	0.41	**Precip12**	0.026	**BIO5**	0.89	**Precip12**	0.014
	BIO11	0.41	**TMin10**	0.025	BIO1	0.88	**BIO7**	0.013
GWWA ♂	BIO11	0.83	Precip03	0.050	**BIO7**	0.99	Precip10	0.024
	BIO6	0.46	Precip10	0.040	BIO6	0.91	**BIO7**	0.021
	BIO7	0.44	**BIO7**	0.038	BIO1	0.89	TMax10	0.019
	BIO1	0.40	Precip12	0.035	BIO5	0.88	Precip03	0.017
WOTH	BIO11	0.93	**BIO7**	0.29	BIO11	1.00	**BIO7**	0.073
	BIO7	0.83	BIO4	0.041	**BIO7**	0.99	BIO4	0.062
	TMin03	0.75	BIO2	0.035	TMin03	0.86	BIO2	0.026
	BIO3	0.68	PFT	0.012	TMin11	0.70	BIO3	0.023

TABLE 3. Total area (km^2) and percent change of suitable climatic and LULC conditions for the focal species in the current timeframe and for each GCCM in the 2050 SSP2-RCP4.5 (best-case) future scenario. Current timeframe is the reference for percent change. Least percent change by 2050 is predicted for *Hylocichla mustelina* (Wood Thrush, WOTH) in the MIROC-ES2L global coupled climate model (–5%). Greatest percent change by 2050 is predicted for female *Vermivora chrysoptera* (Golden-winged Warbler, GWWA ♀) in the FIO-ESM-2-0 global coupled climate model (–75%). Species abbreviations: *Cardellina canadensis* (Canada Warbler, CAWA), *Setophaga cerulea* (Cerulean Warbler, CERW).

		SSP2-RCP4.5 (best-case)		
Species	Current	CMCC-ESM2	FIO-ESM-2-0	MIROC-ES2L
CAWA	259,456	207,521 (–20%)	214,974 (–17%)	240,695 (–7%)
CERW	271,187	174,380 (–36%)	172,427 (–36%)	219,094 (–19%)
GWWA ♀	205,005	60,587 (–71%)	51,665 (–75%)	89,671 (–56%)
GWWA ♂	225,433	91,449 (–59%)	85,773 (–62%)	122,259 (–46%)
WOTH	415,191	336,336 (–19%)	346,769 (–17%)	395,722 (–5%)

longitudinal peak density movement from Honduras (~87° west) to Nicaragua (~85° west) (Supplementary Figure 3e).

Distribution changes

Cardellina canadensis and *S. cerulea* are predicted to lose suitable conditions at lower elevations in the Andes, but *C. canadensis* is predicted to show greater capacity than *S. cerulea* to shift upslope in Ecuador and northern Peru (Figures 2 and 3). *Vermivora chrysoptera* ♀ and ♂ are predicted to lose suitable conditions in many areas of the Neotropics, including Nicaragua and Venezuela (Figure 4). The Gulf-Caribbean slope is predicted to remain suitable for *H. mustelina*, but southern Mexico and the interior of the Yucatán Peninsula may experience noteworthy losses of suitable conditions (Figure 5). See Supplementary Figures 4 to 8 for 6-panel ensemble model comparisons for each focal species.

Comparison of Predicted Occupied Current Ranges to Predicted Current Suitable Conditions

Comparisons between predicted occupied current ranges and predicted current suitable conditions varied by focal species. Predictive method overlap (i.e., predicted current suitable conditions that are currently occupied) was greatest for *C. canadensis* (62%) and least for *V. chrysoptera* ♀ (26%). Areas that are unoccupied but

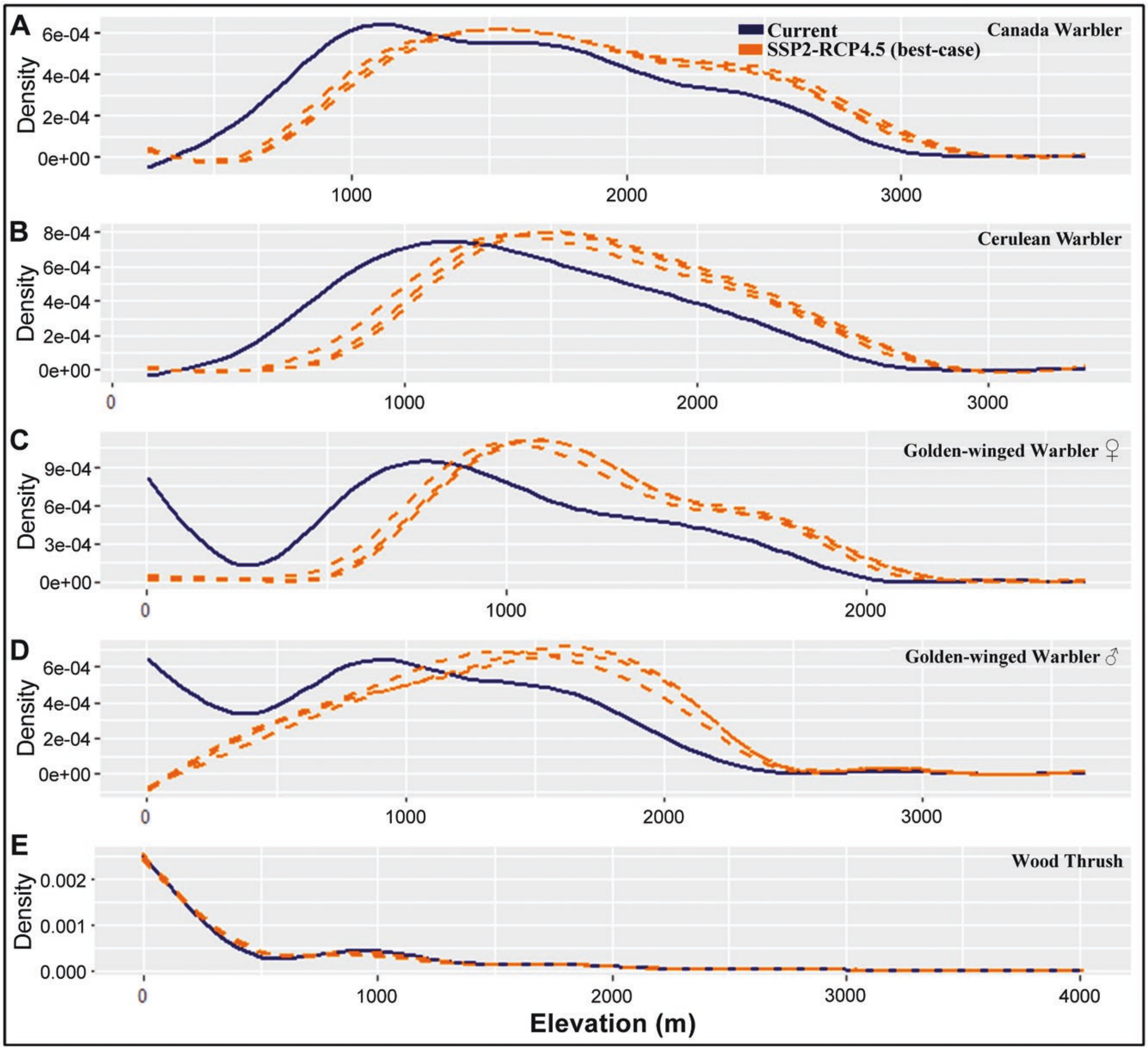

FIGURE 1. Availability of suitable conditions by elevation (m) for (**A**) *C. canadensis*, (**B**) *S. cerulea*, (**C**) female *V. chrysoptera*, (**D**) male *V. chrysoptera*, and (**E**) *H. mustelina* under the 2050 SSP2-RCP4.5 (best-case) climate scenarios (dashed lines) compared to current conditions (solid line). Despite limited elevational shifts in suitable conditions for *H. mustelina*, upslope elevational shifts were predicted for the 3 warbler species. For example, suitable conditions for *C. canadensis* and *S. cerulea* (**A** and **B**) shifted 250 m at the lower elevation limit, and *V. chrysoptera* ♂ (**D**) peak density increased from 900 to 1,500 m.

predicted suitable were relatively small for each species (range: 10% to 33%), while areas that are occupied but predicted to be unsuitable ranged from 14 to 47%. *Cardellina canadensis* occupies predicted unsuitable environments in north-central Peru, whereas large areas with predicted suitable conditions are not currently occupied by *S. cerulea*, particularly at the southern terminus in Peru (Supplementary Figure 9). Patterns were similar between *V. chrysoptera* ♀ and ♂, where large areas of southern Mexico and Central America are currently occupied despite predicted unsuitable conditions (Supplementary Figure 10). Large areas of the Yucatán Peninsula, Honduras, and Nicaragua were areas of overlap between predictive methods for *H. mustelina* (Supplementary Figure 11).

Processes to Identify Near-term Conservation Priority Areas

Despite extensive distribution contractions for *V. chrysoptera* ♀ and ♂ predicted by 2050, 8 Honduran conservation focal areas for ♀ and 6 for ♂ are projected to maintain > 50% area with suitable climatic and LULC conditions (Supplementary Table 5). Average area difference among all Honduran focal areas was –41% for ♀ and –49% for ♂. In the *V. chrysoptera* nonbreeding season conservation plan, focal areas HO06 [La Muralla], HO08 [Sierra de Agalta y El Boqueron], and HO12 [Zona Sur: Biosfera del Rio Platano] have been prioritized due to deforestation threats and the ability of those communities to implement conservation actions (Bennett et al. 2016). HO06 and HO08 are projected to maintain >50% of the area of suitable climatic and LULC conditions for ♀ and ♂, while

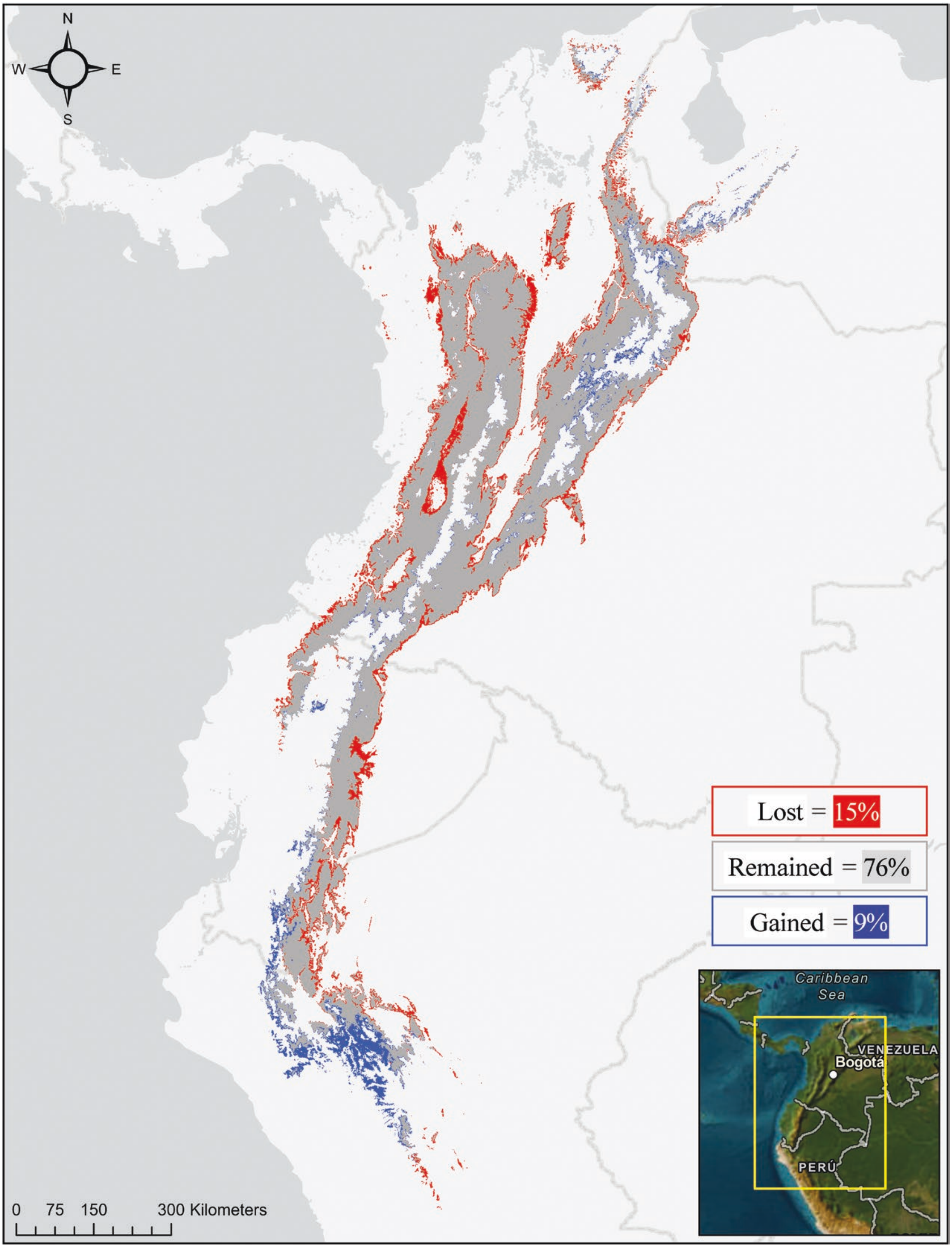

FIGURE 2. Suitable climatic and LULC conditions resulting in areas where *C. canadensis* is projected to be lost, remained, and gained in 2050 under the SSP2-RCP4.5 (best-case) MIROC-ES2L climate scenario. Areas remained suggested that suitable conditions will be stable throughout the species' stationary nonbreeding distribution. *Cardellina canadensis* may have the capacity to shift upslope in portions of southern Ecuador and north-central Peru. However, the Colombian Andes west of Bogotá were predicted to lose suitable conditions at lower elevations. Results predict a 6% net loss of suitable climatic and LULC conditions.

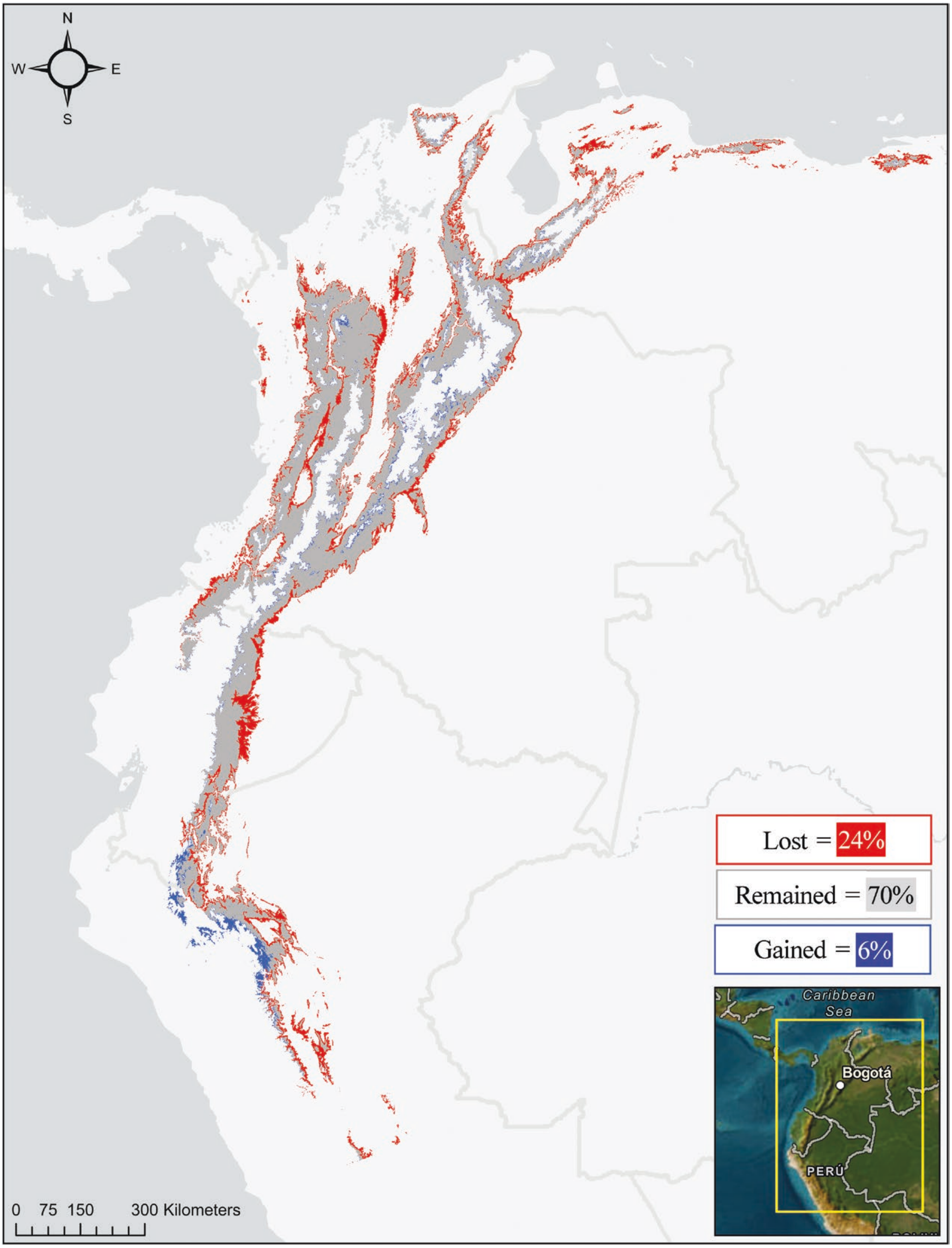

FIGURE 3. Suitable climatic and LULC conditions resulting in areas where *S. cerulea* is projected to be lost, remained, and gained in 2050 under the SSP2-RCP4.5 (best-case) MIROC-ES2L climate scenario. Results predict an 18% net loss of suitable conditions in which loss will primarily occur in north-central Peru and along lower elevation edges of stable conditions from the northern to southern termini of the distribution. Despite predictions suggesting there will be minimal gain in suitable conditions in the northern Andes, *S. cerulea* may be able to shift upslope to higher elevations in northern Peru by 2050.

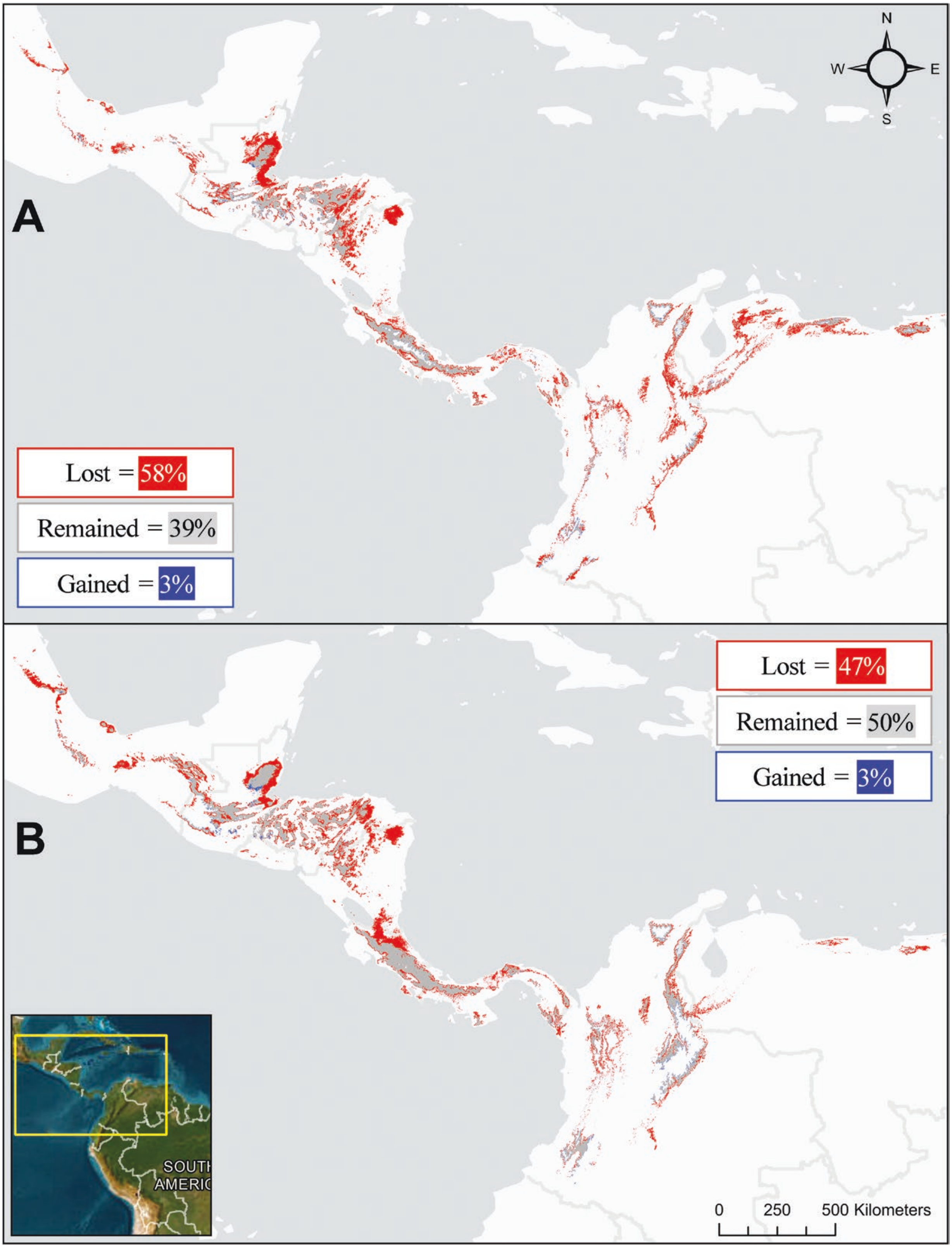

FIGURE 4. Suitable climatic and LULC conditions resulting in areas where *V. chrysoptera* (**A**) ♀ and (**B**) ♂ are projected to be lost, remained, and gained in 2050 under the SSP2-RCP4.5 (best-case) MIROC-ES2L climate scenario. Areas remained suggested that stable suitable conditions in the Belize interior and Costa Rica will persist for both sexes. Patches of remaining suitable areas in Honduras will be interspersed with unsuitable environments. Results predict a net loss (55% for ♀, 44% for ♂) of suitable conditions by 2050, where loss may be most severe for Appalachian breeding *V. chrysoptera* ♀ in the northern Andes.

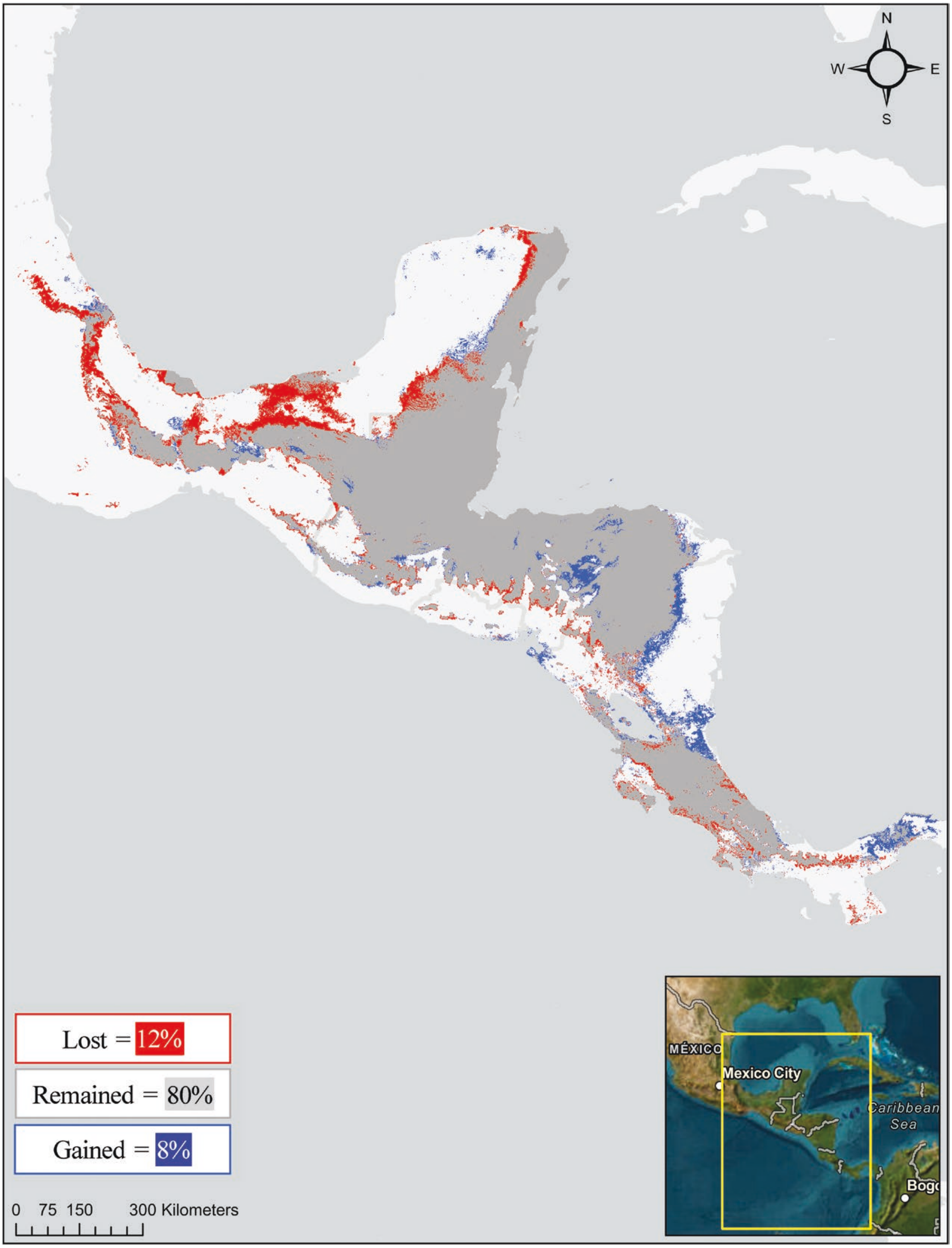

FIGURE 5. Suitable climatic and LULC conditions resulting in areas where *H. mustelina* is projected to be lost, remained, and gained in 2050 under the SSP2-RCP4.5 (best-case) MIROC-ES2L climate scenario. Areas remained suggested there will be stable suitable conditions throughout the species' stationary nonbreeding distribution. Results predict a 4% net loss of suitable climatic and LULC conditions in which changing conditions in southern Mexico and the Yucatán Peninsula interior are mostly responsible. Along the edges of stable suitable conditions in Nicaragua, *H. mustelina* may have the opportunity to slightly expand its distribution east by 2050.

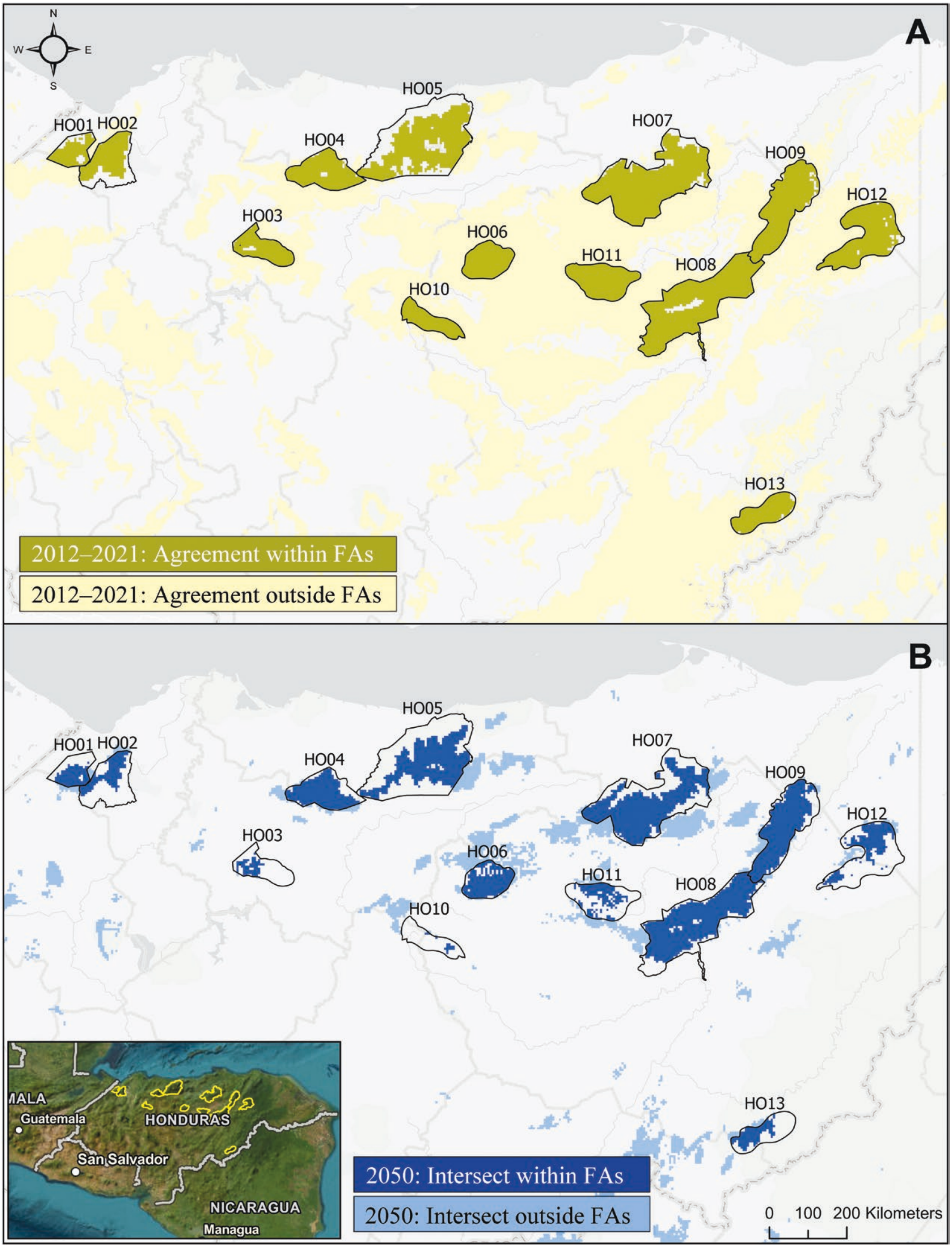

FIGURE 6. *Vermivora chrysoptera* ♀ comparisons within and outside Honduran conservation focal areas (FAs) for (**A**) predictive method overlaps (currently occupied areas that have suitable climatic and LULC conditions) in the current timeframe and (**B**) the intersection of all SSP2-RCP4.5 (best-case) 2050 projections. Thirteen Honduran conservation FAs (Bennett et al. 2016) are outlined in black with area IDs. In the current timeframe, all areas within HO06, HO10, and HO11 are predicted to be currently suitable for and occupied by *V. chrysoptera* ♀. Results indicate that HO09 will only lose 13% of the area of suitable climatic and LULC conditions by 2050.

HO12 is projected to only maintain 39% for ♀ and 42% for ♂ by 2050 (Supplementary Table 5). Visual representations revealed suitable landscapes for potential expansion outside delineated focal areas, while future projection intersections displayed feasible areas of expansion in the near-term (Figure 6).

DISCUSSION

Predicted Distribution Changes for Focal Species

By 2050, our results predict that the distribution of suitable conditions will contract for each focal bird species and shift upslope in elevation for the 3 warbler species. To support the ecological phenomenon of an "escalator to extinction" (Freeman et al. 2018), suitable conditions at lower elevations must become unsuitable, shifts in the upper elevation limit must be negligible, and a narrower elevation range must be realized. Our findings support this given that the 3 warbler species are expected to track their ecological niche to higher elevations but not extend their upper elevation limit, greatly reducing their potential distribution. The lower elevation limit for *C. canadensis*, *S. cerulea*, and *V. chrysoptera* ♀ is expected to increase with no obvious change to the upper elevation limit. Though *V. chrysoptera* ♂ remained at their current lower elevational range in lower densities, their peak density is projected to shift higher (1,500 m). In contrast, suitable conditions for *H. mustelina* are expected to remain relatively unchanged with minimal distribution shifts in elevation. Flexible habitat selection exhibited locally by *H. mustelina* (Bailey and King 2019, Stanley et al. 2021) likely extends to broader tracking of changes in climatic and LULC conditions.

Vermivora chrysoptera displays habitat segregation by sex during the stationary nonbreeding period, where ♀ and ♂ occupy elevations between 300 and 1,300 m and between 800 and 1,800 m, respectively (Bennett et al. 2019). Our analyses suggest that habitat overlap will expand under future climatic and LULC conditions, where the narrower *V. chrysoptera* ♀ elevation range is predicted to fall entirely within the range for ♂. Yet, intraspecies competition is believed to displace ♀ and young ♂ to suboptimal habitats (Bennett et al. 2019), which may prevent these groups from tracking suitable conditions. Additionally, differences in elevational peak density shifts between ♀ (400 m) and ♂ (600 m) may be an indicator of sex-specific risk, where *V. chrysoptera* ♂ are predicted to persist in higher elevation environments with limited space and resources (Gómez et al. 2015). Due to recent planning bias for ♂ at high elevations which fails to include important areas for ♀ (Bennett et al. 2019), sex-specific responses must be accounted for in future conservation strategies. We were able to model ♀ and ♂ separately because *V. chrysoptera* is a sexually dimorphic species. Sex is difficult to differentiate in the other 3 focal species as males and females appear the same; thus, modeling sex-specific responses was not feasible, though this is a critical area for future research.

Histograms for availability of future suitable conditions showed only slight latitudinal and longitudinal shifts. This observation is consistent with weak latitudinal temperature gradients in the Neotropics (Colwell et al. 2008, Freeman et al. 2018), and that some species respond more strongly to pronounced temperature changes across elevational gradients (Céspedes Arias et al. 2022). Minimal longitudinal and latitudinal dispersal exhibited by *C. canadensis* and *S. cerulea* reinforce the importance of conservation action in montane regions of the Ecuadorian and Colombian Andes which hold the core stationary nonbreeding distributions for both species (Rodríguez et al. 2013). The same is true for *V. chrysoptera* in Costa Rica, where suitable conditions are predicted to remain despite notable contraction elsewhere. For *H. mustelina*, the most northerly and lowland-associated focal species, small shifts in latitude and longitude may be a response to limited interactions with strong elevational temperature gradients.

Drivers of Focal Bird Species Distribution Changes

Temperature metrics best explained stationary nonbreeding distribution shifts for 3 of 4 declining Neotropical migratory forest birds. For *C. canadensis* and *S. cerulea*, monthly temperatures at the onset of our defined stationary nonbreeding periods were important predictors. Minimum and maximum temperatures in October and November may influence site selection for these species which are influenced by strong elevational temperature gradients (Céspedes Arias et al. 2022). For *H. mustelina*, temperature annual range (i.e., BIO7) was an important predictor, which is supported by the species' flexible habitat selection between 50 and 1,000 m elevation (Bailey and King 2019, Evans et al. 2020).

Monthly precipitation covariates were influential in explaining projected distribution shifts for *V. chrysoptera* ♀ and ♂, which aligns with recent studies that indicated Neotropical migrants track precipitation patterns as they seek resources (MacPherson et al. 2018, Stanley et al. 2021). Precipitation affects the development of epiphytes which *V. chrysoptera* use to forage for insects in disturbed mid-elevation forests (Roth et al. 2019). We expected precipitation metrics to play a greater role in projections for *C. canadensis*, *S. cerulea*, and *H. mustelina* given that Neotropical migrants exhibit strong associations to precipitation regimes and moisture in soil and tree canopies (Bennett et al. 2019, Stanley et al. 2021, Céspedes Arias et al. 2022). Notably for *H. mustelina*, facultative movements in Belize are contingent on local-scale patterns of moisture (Stanley et al. 2021). The temporal resolution of our precipitation covariates may be too coarse to reflect seasonal rainfall variations across our study's spatial extent for most species. Our modeling framework could be applied at local scales where it would then be possible to include additional covariates such as seasonal rainfall, effects of the El Niño Southern Oscillation (Paxton et al. 2014) and land management (González et al. 2023b).

Resilience to LULC change for mixed species flocks (Jernakoff et al. 2023) may explain why plant functional types (PFT) were less influential in our ensemble models for the 3 warbler species. Joining a mixed species flock can be advantageous for species vulnerable to landscape disturbance, particularly if a nuclear bird species drives high functional diversity (Williams and Lindell 2019, Jernakoff et al. 2023). The 3 warbler species may also benefit from shared contributions to changing ecological processes, as climatically vulnerable species with similar functional traits are most at risk of population decline (Germain et al. 2023). In contrast, PFT was more informative for *H. mustelina* possibly because the species is solitary in the Neotropics (Stanley et al. 2021). Additionally, estimations of available suitable conditions by elevation suggested that PFT set a maximum elevational constraint on suitable LULC types in future projections. For example, the upper elevation limits for suitable conditions only moved from 3,100 to 3,250 m for *C. canadensis* and from 2,750 to 2,900 m for *S. cerulea*. However, the forest and agroforest ecosystems which these species rely on persist only to 3,250 m in the northern Andes, where forest transitions to páramo (Céspedes Arias et al. 2022).

Do Predictions of Occupied Current Ranges and Current Suitable Conditions Coincide?

Areas of predictive overlap, where suitable conditions are likely to remain, may be the most reliable places to focus near-term conservation efforts in the Neotropics. However, there were substantial areas of current suitable conditions not currently occupied. These areas (i.e., green in Supplementary Figures 9 to 11) represent potential habitat; however, with species known to be in recent decline, these areas may be vacant due to population declines resulting in fewer individual birds occupying suitable landscapes and may not become occupied if populations continue to decline. Additionally, these areas may not be occupied due to (1) inclusion of migratory occurrence records despite our attempts to eliminate them, (2) birds having not yet shifted to these areas given their site fidelity and dispersal dynamics, (3) suitable conditions at finer scales than our analysis that allow for local persistence, (4) other important habitat characteristics not included in our models that are absent in these geographic areas, and (5) poor understanding of the intrinsic mechanisms (e.g., physiological) that drive individuals and populations to shift across the landscape. Areas that are unsuitable but currently occupied (i.e., purple in Supplementary Figures 9 to 11) may be areas of concern as near-term distribution contractions could lead to local extirpations.

Overlap between occupied current range and our predictions of current suitable conditions was smallest for *V. chrysoptera*. This species exhibits strong migratory connectivity and site fidelity (Hobson et al. 2016, Kramer et al. 2017, Roth et al. 2019), which may result in individuals continuing to occupy areas that are increasingly unsuitable. In this case, it would be reasonable to consider conservation action in known occupied areas, though occupied areas that are predicted to be suitable could be prioritized as more important. Additionally, many of the currently suitable but unoccupied areas in South America are occupied at low densities. These areas were lost in this analysis due to higher *V. chrysoptera* densities in Central America and removal of abundance values < 0.1. Stark differences in density between regions were addressed in prior CIS analyses by modeling the 2 *V. chrysoptera* regional populations separately (González et al. 2023a). Therefore, our sex-specific analyses could be conducted for each regional population.

Strategies to Identify Near-Term Conservation Priority Areas

Results from this study can be used to improve conservation of the 4 focal bird species and can be applied to other multi-species migratory and resident conservation approaches. We suggest 2 strategies for directing limited resources to areas where the focal species are likely to benefit. First, to maintain currently suitable landscapes, the process developed in this study could be used to identify priority focal areas. Existing focal area boundaries could also be evaluated for expansion. For species without focal areas, this process may help delineate them for the first time. Second, to conserve areas likely to be suitable in the future regardless of current suitability, strategists should consider allocating resources to areas of overlap among future projections. Projections of climate and LULC vary (Riahi et al. 2017), and areas of overlap among projections represented the locations most likely to be suitable by 2050. Considering the lack of resources for conservation in the Neotropics (González et al. 2023b), this approach can be used by practitioners to allocate limited resources to areas predicted to maintain suitable conditions.

The mid-elevation forest CIS emphasized *V. chrysoptera* conservation action between 600 and 1,800 m in Honduras and Costa Rica (González et al. 2023a). Our *V. chrysoptera* results suggest that practitioners direct most conservation resources to Honduras, given high deforestation rates there and the favorable state of mid-elevation forests in Costa Rica (González et al. 2023a). Conservation action in these degrading habitats may also help to restore fitness and fecundity for *V. chrysoptera* during the breeding season (Kramer et al. 2017, La Sorte et al. 2017) and protect stopover landscapes for *C. canadensis*, *S. cerulea*, and Appalachian *V. chrysoptera*s migrating to South America (González et al. 2023a). Our results revealed that conservation focal areas in Honduras (Bennett et al. 2016) were delineated appropriately with minor exceptions. Following the first strategy above, 3 focal areas (i.e., HO06, HO08, HO12) should remain priorities with expansion opportunities in areas surrounding HO06. Following the second strategy, focal area HO12 could be reduced as a priority due to observable losses of suitable climatic and LULC conditions. Expansion would only be feasible for areas directly north of HO06.

Conclusions

Over the next 20 to 40 years, we predict notable distribution contractions for 3 of 4 Neotropical migrant bird species as suitable climatic and LULC conditions shift, and particularly as they become constrained by narrower elevation limits. It is essential to extend this research to 2100 as climatic and LULC projections among SSP-RCPs may diverge notably beyond 2050 (Van Vuuren et al. 2011, Riahi et al. 2017). To better understand drivers of population decline, there is an urgent need for full-annual cycle CISs to consider demographic information in distribution models (Wilson et al. 2018). For species which exhibit strong migratory connectivity, currently suitable but unoccupied areas may provide insights into species demographics on the breeding grounds, such as if production and recruitment are insufficient to produce enough individuals to occupy all suitable stationary nonbreeding habitat. Additionally, continental predictions of distribution shifts should be combined with local-scale information, including threats, protected areas, and indigenous reserves (González et al. 2023b). Conservation focal areas are working landscapes shared by birds and people, including farmers and indigenous communities. The successful execution of conservation objectives, including those identified in CISs and other plans, will depend entirely on direct engagement with communities across these working landscapes.

Supplementary material

Supplementary material is available at *Ornithological Applications* online.

Acknowledgments

We are grateful to Kurt Ongman for assisting in grant development and are appreciative of eBird, Ruth Bennett, and the USGS Bird Banding Laboratory for providing bird occurrence data. The authors thank A. Ash, R. B. McNab, D. Becker, O. Bermudez, M. Charette, L. C. Duriaux, M. Chávez, T. Christensen, G. Duriaux, J. Furchgott, O. G. Palacios, V. Galan, D. Hamilton, J. Herner-Thogmartin, The Institute for Bird Populations, O. Jarquín, E. Kay, Lifenet Nature, A. M. Salinas, R. Mendietta, L. Moreno, S. Otterstrom, F. Rodríguez, M. Sotelo, M. Torres, P. Torres, M. Torrez, and J. M. Zolotoff. Support for stations run by CATIE in Costa Rica came from the U.S. Fish and Wildlife Service, Idea Wild, The Tropics Foundation, Optics for the Tropics, Perennial Crop Platform, Wallace Genetic Foundation, Biodiversity International, and private donors. We also thank over 100 volunteers who helped the MoSI program collect data. Special thanks to A. M. Rodríguez and CATIE authorities who allowed the use of CATIE property. In addition, thank you to Erin Simons-Legaard, Sydne Record, and the reviewers for manuscript improvement.

Funding statement

Research was funded by Environment and Climate Change Canada and the U.S. Fish and Wildlife Service Midwest Migratory Bird Program (grant no. F23AP00143). Additional support was provided by the Maine Agricultural and Forest Experiment Station (project no. ME042018).

Ethics statement

We used data from online databases (eBird) and species-specific field studies (Supplementary Table 1). All protocols established by these databases and studies were followed appropriately.

Conflict of interest statement

The authors declare no conflict of interest.

Author contributions

REB, AMR, NJB, JH, and RLMS conceived the idea; REB, NJB, and JH developed the methods; JLL and AMG collected data; REB analyzed the data and performed the experiments; REB, AMR, NJB, AMG, JH, JLL, RLMS, and SW wrote the paper; AMR and RLMS contributed substantial resources and funding.

Data availability

Analyses in this article can be reproduced using the data provided by Brodie et al. (2024).

Collaboration Ethics Statement

Nonbreeding distributions of four declining Nearctic-Neotropical migrants are predicted to contract under future climate and socioeconomic scenarios

The corresponding author and co-authors of this research confirm that local, on-the-ground studies in the Neotropics were principally important during methodological development. We were cognizant of the state and needs of conservation in this region during formation of discussion talking points. Although we were unable to represent authorship from each country in the Neotropics that this study intersected with, several co-authors have either in-country research experience, native citizenship, or both. To name a few, Nicholas J. Bayly is Director of the Migratory Ecology program at SELVA Investigación para la Conservación en el Neotropico and oversees many nonbreeding and migratory ecology projects. Ana M. González is native to Colombia and has published many papers detailing nonbreeding and migratory dynamics of forest birds experiencing population decline. The goal of this study was to develop processes to identify conservation priority areas in the Neotropics, but we understood that continental distribution projections must be coupled with local, on-the-ground knowledge. We provided an example of this process by intersecting our distribution projections with delineated Honduran focal areas in the Golden-winged Warbler nonbreeding season conservation plan (Bennett et al. 2016). Upon article acceptance, the code, response and covariate data, and products from this study will be made available via Dryad for public use. Additionally, the U.S. Fish and Wildlife Service Midwest Migratory Bird Program (grant no. F23AP00143) requires the corresponding author to develop a decision support tool to assist strategists with conservation planning. The tool will be produced using the *shiny* package in R and feature maps from this study, protected areas, predelineated focal areas, etc. to assist in decision making. The tool's hyperlink can be added to any website for easy access. We hope that the decision support tool makes it easier for researchers in the Neotropics to implement their own research agendas.

LITERATURE CITED

Acevedo, P., J. Melo-Ferreira, R. Real, and P. C. Alves (2012). Past, present and future distributions of an Iberian endemic, *Lepus granatensis*: Ecological and evolutionary clues from species distribution models. *PLoS One* 7:1–11.

Almazroui, M., M. Ashfaq, M. N. Islam, I. U. Rashid, S. Kamil, M. A. Abid, E. O'Brien, M. Ismail, M. S. Reboita, A. A. Sörensson, et al. (2021). Assessment of CMIP6 performance and projected temperature and precipitation changes over South America. *Earth Systems and Environment* 5:155–183.

Araújo, M., and M. New (2007). Ensemble forecasting of species distributions. *Trends in Ecology & Evolution* 22:42–47.

Bailey, B. A., and D. I. King (2019). Habitat selection and habitat quality for wintering Wood Thrushes in a coffee growing region in Honduras. *Global Ecology and Conservation* 20:e00728.

Bao, Y., Z. Song, and F. Qiao (2020). FIO-ESM Version 2.0: Model description and evaluation. *Journal of Geophysical Research: Oceans* 125:e2019JC016036.

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.

Bax, V., A. Castro-Nunez, and W. Francesconi (2021). Assessment of potential climate change impacts on montane forests in the Peruvian Andes: Implications for conservation prioritization. *Forests* 12:375.

Bennett, R.E., A. Rothman, K. V. Rosenberg, and F. Rodriguez (2016) Golden-winged Warbler non-breeding season conservation plan. In

Golden-winged Warbler Status Review and Conservation Plan (A. M. Roth, R. W. Rohrbaugh, T. Will, and D. A. Buehler, Editors). Golden-winged Warbler Working Group, www.gwwa.org.

Bennett, R. E., A. D. Rodewald, and K. V. Rosenberg (2019). Overlooked sexual segregation of habitats exposes female migratory landbirds to threats. *Biological Conservation* 240:108266.

Botero-Delgadillo, E., S. Escudero-Páez, J. Sanabria-Mejía, P. Caicedo, and N. J. Bayly (2022). Sequential use of niche and occupancy models identifies conservation and research priority areas for two data-poor endemic birds from the Colombian Andes. *Ornithological Applications* 124:duab063.

Brodie, R. E., N. J. Bayly, A. M. González, J. Hightower, J. L. Larkin, R. L. M. Stewart, S. Wilson, and A. M. Roth (2024). Data from: Nonbreeding distributions of four declining Nearctic–Neotropical migrants are predicted to contract under future climate and socioeconomic scenarios. *Ornithological Applications* 126:duae032. doi:10.5061/dryad.g1jwstr0h [Dataset].

Brown, J. L., and A. D. Yoder (2015). Shifting ranges and conservation challenges for lemurs in the face of climate change. *Ecology and Evolution* 5:1131–1142.

Bucklin, D. N., M. Basille, A. M. Benscoter, L. A. Brandt, F. J. Mazzotti, S. S. Romañach, C. Speroterra, and J. I. Watling (2015). Comparing species distribution models constructed with different subsets of environmental predictors. *Diversity and Distributions* 21:23–35.

Buehler, D. A., P. B. Hamel, and T. Boves (2020). Cerulean Warbler (*Setophaga cerulea*), version 1.0. In *Birds of the World* (A. F. Poole, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. doi:10.2173/bow.cerwar.01

Céspedes Arias, L. N., S. Wilson, and N. J. Bayly (2022). Community modeling reveals the importance of elevation and land cover in shaping migratory bird abundance in the Andes. *Ecological Applications* 32:e02481.

Chen, G., X. Li, and X. Liu (2022). Global land projection based on plant functional types with a 1-km resolution under socio-climatic scenarios. *Scientific Data* 9:125.

Cherchi, A., P. G. Fogli, T. Lovato, D. Peano, D. Iovino, S. Gualdi, S. Masina, E. Scoccimarro, S. Materia, A. Bellucci, and A. Navarra (2019). Global mean climate and main patterns of variability in the CMCC-CM2 coupled model. *Journal of Advances in Modeling Earth Systems* 11:185–209.

Colorado, G. J., P. B. Hamel, A. D. Rodewald, and D. Mehlman (2012). Advancing our understanding of the non-breeding distribution of Cerulean Warbler (*Setophaga Cerulea*) in the Andes. *Ornitologia Neotropical* 23:307–315.

Colwell, R. K., G. Brehm, C. L. Cardelús, A. C. Gilman, and J. T. Longino (2008). Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. *Science* 322:258–261.

Confer, J. L., P. Hartman, and A. Roth (2020). Golden-winged Warbler (*Vermivora chrysoptera*), version 1.0. In *Birds of the World* (A. F. Poole, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. doi:10.2173/bow.gowwar.01

Da Silveira, N. S., M. H. Vancine, A. E. Jahn, M. A. Pizo, and T. Sobral-Souza (2021). Future climate change will impact the size and location of breeding and wintering areas of migratory thrushes in South America. *Ornithological Applications* 123:duab006.

Dray, S., A. B. Dufour, and J. Thioulouse (2023). *ade4: Analysis of ecological data: exploratory and euclidean methods in environmental sciences*. R package version 1.7-22. https://cran.r-project.org/web/packages/ade4/index.html

Esri Inc. (2022). *ArcGIS Pro. Esri Inc., Redlands, CA*, USA.

Evans, M., E. Gow, R. R. Roth, M. S. Johnson, and T. J. Underwood (2020). Wood Thrush (*Hylocichla mustelina*), version 1.0. In *Birds of the World* (A. F. Poole, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. doi:10.2173/bow.woothr.01

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

Fink, D., T. Auer, A. Johnston, M. Strimas-Mackey, S. Ligocki, O. Robinson, W. Hochachka, L. Jaromczyk, A. Rodewald, C. Wood, I. Davies, and A. Spencer (2022). *eBird Status and Trends, Data Version: 2021; Released: 2022*. Cornell Lab of Ornithology, Ithaca, New York. doi:10.2173/ebirdst.2021

Fontúrbel, F. E., J. F. Betancurt-Grisales, A. M. Vargas-Daza, and G. J. Castaño-Villa (2022). Effects of habitat degradation on bird functional diversity: A field test in the Valdivian rainforest. *Forest Ecology and Management* 522:120466.

Fotheringham, A. S., and T. M. Oshan (2016). Geographically weighted regression and multicollinearity: Dispelling the myth. *Journal of Geographical Systems* 18:303–329.

Freeman, B. G., M. N. Scholer, V. Ruiz-Gutierrez, and J. W. Fitzpatrick (2018). Climate change causes upslope shifts and mountaintop extirpations in a tropical bird community. *Proceedings of the National Academy of Sciences USA* 115:11982–11987.

Fuentes-Franco, R., E. Coppola, F. Giorgi, F. Graef, and E. G. Pavia (2014). Assessment of RegCM4 simulated inter-annual variability and daily-scale statistics of temperature and precipitation over Mexico. *Climate Dynamics* 42:629–647.

Germain, R. R., S. Feng, L. Buffan, C. P. Carmona, G. Chen, G. R. Graves, J. A. Tobias, C. Rahbek, F. Lei, J. Fjeldså, P. A. Hosner, M. T. Gilbert, G. Zhang, and D. Nogués-Bravo (2023). Changes in the functional diversity of modern bird species over the last million years. *Proceedings of the National Academy of Sciences USA* 120:e2201945119.

Gómez, C., V. Gómez-Bahamón, L. Cárdenas-Ortíz, and N. J. Bayly (2015). Distribution of Nearctic–Neotropical migratory birds along a South American elevation gradient during spring migration. *The Wilson Journal of Ornithology* 127:72–86.

Gómez, C., and S. Flores (2023). eBird Status and trends_StefanyFlores.R. In *Priorizacion-Bosques-Elevaciones-Medias*. GitHub Repository. https://github.com/camilgomo/Priorizacion-Bosques-Elevaciones-Medias/blob/2848d48d49d666b917128d361b427caad5b6d8b2/eBird%20Status%20and%20trends_StefanyFlores.R

González, A. M., N. Bayly, E. Secaira, R. Miro, Y. L. Diaz, M. A. Meneses, S. Escudero, R. Dettmers, and B. Stewart (2023a). *Conservation Investment Strategy for the mid-elevation forests of Central and South America*. Partners in Flight.

González, A. M., N. Espejo, D. Armenteras, K. A. Hobson, K. J. Kardynal, G. W. Mitchell, N. Mahony, C. A. Bishop, P. J. Negret, and S. Wilson (2023b). Habitat protection and restoration: Win–win opportunities for migratory birds in the northern Andes. *Perspectives in Ecology and Conservation* 21:33–40.

González-Prieto, A. M., N. J. Bayly, G. J. Colorado, and K. A. Hobson (2017). Topography of the Andes Mountains shapes the wintering distribution of a migratory bird. *Diversity and Distributions* 23:118–129.

Groves, C. R., E. T. Game, M. G. Anderson, M. Cross, C. Enquist, Z. Ferdaña, E. Girvetz, A. Gondor, K. R. Hall, J. Higgins, R. Marshall, K. Popper, S. Schill, and S. L. Shafer (2012). Incorporating climate change into systematic conservation planning. *Biodiversity and Conservation* 21:1651–1671.

Guisan, A., W. Thuiller, and N. E. Zimmermann (2017). *Habitat Suitability and Distribution Models with Applications in R*. Cambridge University Press, Cambridge, UK.

Hajima, T., M. Watanabe, A. Yamamoto, H. Tatebe, M. A. Noguchi, M. Abe, R. Ohgaito, A. Ito, D. Yamazaki, H. Okajima, A. Ito, K. Takata, K. Ogochi, S. Watanabe, and M. Kawamiya (2020). Development of the MIROC-ES2L Earth system model and the evaluation of biogeochemical processes and feedbacks. *Geoscientific Model Development* 13:2197–2244.

Hightower, J. N., D. L. Crawford, W. E. Thogmartin, K. R. Aldinger, S. B. Swarthout, D. A. Buehler, J. Confer, C. Friis, J. L. Larkin, J. D. Lowe, M. Piorkowski, R. W. Rohrbaugh, K. V. Rosenberg, C. Smalling, P. B. Wood, R. Vallender, and A. M. Roth (2023). Change in climatically suitable breeding distributions reduces hybridization potential between *Vermivora* warblers. *Diversity and Distributions* 29:254–271.

Hobson, K. A., S. L. Van Wilgenburg, A. M. Roth, R. E. Bennett, N. J. Bayly, L. Chavarría-Duriaux, G. J. Colorado, P. Elizondo, C. G. Rengifo, and J. D. Ritterson. (2016). Golden-winged Warbler migratory connectivity derived from stable isotopes. In *Golden-winged Warbler Ecology, Conservation, and Habitat Management* (H. M. Streby, D. E. Andersen, and D. A. Buehler, Editors). Studies in Avian Biology (no. 49), CRC Press, Boca Raton, FL, USA. pp. 193–203.

Jernakoff, M., J. Knowlton, B. Vásquez-Ávila, C. Espinosa, and B. Tinoco (2023). Effects of land use change on the functional diversity and composition of mixed species avian flocks in the high tropical Andes of southern Ecuador. *Journal of Field Ornithology* 94:art3.

Kramer, G. R., H. M. Streby, S. M. Peterson, J. A. Lehman, D. A. Buehler, P. B. Wood, D. J. McNeil, J. L. Larkin, and D. E. Andersen (2017). Nonbreeding isolation and population-specific migration patterns among three populations of Golden-winged Warblers. *The Condor: Ornithological Applications* 119:108–121.

La Sorte, F. A., D. Fink, P. J. Blancher, A. D. Rodewald, V. Ruiz-Gutierrez, K. V. Rosenberg, W. M. Hochachka, P. H. Verburg, and S. Kelling (2017). Global change and the distributional dynamics of migratory bird populations wintering in Central America. *Global Change Biology* 23:5284–5296.

MacPherson, M. P., A. E. Jahn, M. T. Murphy, D. H. Kim, V. R. Cueto, D. T. Tuero, and E. D. Hill (2018). Follow the rain? Environmental drivers of *Tyrannus* migration across the New World. *The Auk: Ornithological Advances* 135:881–894.

Maggini, R., A. Lehmann, M. Kéry, H. Schmid, M. Beniston, L. Jenni, and N. Zbinden (2011). Are Swiss birds tracking climate change? *Ecological Modelling* 222:21–32.

Mariano-Neto, E., and R. A. S. Santos (2023). Changes in the functional diversity of birds due to habitat loss in the Brazil Atlantic Forest. *Frontiers in Forests and Global Change* 6: 1041268.

Marra, P. P., E. B. Cohen, S. R. Loss, J. E. Rutter, and C. M. Tonra (2015). A call for full annual cycle research in animal ecology. *Biology Letters* 11:20150552.

Medina, W., R. M. Huang, and S. L. Pimm (2023). Region-wide retreats from lower elevations of range-restricted birds across the northern Andes. *Conservation Biology* 37:e14127.

Morales, S., E. Montenegro-Pazmiño, and Y. Diaz (2022). *Investment Plan for the Conservation of Resident and Migratory Land Birds on the Caribbean Slope*. Birdlife International, Audubon Panamá, Quito, Ecuador.

Paxton, K. L., E. B. Cohen, E. H. Paxton, Z. Németh, and F. R. Moore (2014). El Niño-Southern Oscillation is linked to decreased energetic condition in long-distance migrants. *PLoS One* 9:e95383.

Qiao, H., J. Soberón, and A. T. Peterson (2015). No silver bullets in correlative ecological niche modelling: Insights from testing among many potential algorithms for niche estimation. *Methods in Ecology and Evolution* 6:1126–1136.

R Core Team (2022). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Reitsma, L. R., M. T. Hallworth, M. McMahon, and C. J. Conway (2020). Canada Warbler (*Cardellina canadensis*), version 2.0. In *Birds of the World* (P. G. Rodewald and B. K. Keeney, Editors). Cornell Lab of Ornithology, Ithaca, NY, USA. doi:10.2173/bow.canwar.02

Riahi, K., D. P. Van Vuuren, E. Kriegler, J. Edmonds, B. C. O'Neill, S. Fujimori, N. Bauer, K. Calvin, R. Dellink, O. Fricko, et al. (2017). The Shared Socioeconomic Pathways and their energy, land use, and greenhouse gas emissions implications: An overview. *Global Environmental Change* 42:153–168.

Rodríguez, N., D. Armenteras, and J. Retana (2013). Effectiveness of protected areas in the Colombian Andes: Deforestation, fire and land-use changes. *Regional Environmental Change* 13:423–435.

Rosenberg, K. V., A. M. Dokter, P. J. Blancher, J. R. Sauer, A. C. Smith, P. A. Smith, J. C. Stanton, A. Panjabi, L. Helft, M. Parr, and P. P. Marra (2019). Decline of the North American avifauna. *Science* 366:120–124.

Roth, A. M., R. W. Rohrbaugh, T. Will, S. Barker Swarthout, and D. A. Buehler, editors (2019). *Golden-winged Warbler Status Review and Conservation Plan*, 2nd Edition. www.gwwa.org.

Sánchez-Nivicela, M., and E. Montenegro-Pazmiño (2022). *Conservation Investment Strategy for Resident and Migrant Birds in the Chocó of Northwestern Ecuador*. Birdlife International, Aves y Conservación, Fundación Jocotoco, Quito, Ecuador.

Sekercioglu, C. H., S. H. Schneider, J. P. Fay, and S. R. Loarie (2008). Climate change, elevational range shifts, and bird extinctions. *Conservation Biology* 22:140–150.

Soares, L., K. L. Cockle, E. Ruelas Inzunza, J. T. Ibarra, C. I. Miño, S. Zuluaga, E. Bonaccorso, J. C. Ríos-Orjuela, F. A. Montaño-Centellas, J. F. Freile, et al. (2023). Neotropical ornithology: Reckoning with historical assumptions, removing systemic barriers, and reimagining the future. *Ornithological Applications* 125:duac046.

Stanley, C. Q., M. R. Dudash, T. B. Ryder, W. Gregory Shriver, and P. P. Marra (2021). Variable tropical moisture and food availability underlie mixed winter space-use strategies in a migratory songbird. *Proceedings of the Royal Society B: Biological Sciences* 288:20211220.

Strimas-Mackey, M., E. Miller, and W. Hochachka (2018). *auk: eBird Data Extraction and Processing with AWK*. R package version 0.3.0. https://cornelllabofornithology.github.io/auk/

Strimas-Mackey, M., S. Ligocki, T. Auer, and D. Fink (2023). *ebirdst: Access and Analyze eBird Status and Trends Data*. R package version 2.2021.3. https://github.com/ebird/ebirdst

Sullivan, B. L., C. L. Wood, M. J. Iliff, R. E. Bonney, D. Fink, and S. Kelling (2009). eBird: A citizen-based bird observation network in the biological sciences. *Biological Conservation* 142:2282–2292.

Thuiller, W., B. Lafourcade, R. Engler, and M. B. Araújo (2009). BIOMOD—A platform for ensemble forecasting of species distributions. *Ecography* 32:369–373.

Tingley, M. W., M. S. Koo, C. Moritz, A. C. Rush, and S. R. Beissinger (2012). The push and pull of climate change causes heterogeneous shifts in avian elevational ranges. *Global Change Biology* 18:3279–3290.

Van Vuuren, D. P., J. Edmonds, M. Kainuma, K. Riahi, A. Thomson, K. Hibbard, G. C. Hurtt, T. Kram, V. Krey, J.-F Lamarque, T. Masui, M. Meinshausen, N. Nakicenovic, S. J. Smith, and S. K. Rose (2011). The representative concentration pathways: An overview. *Climatic Change* 109:5–31.

Whitney, C. K., W. W. L. Cheung, and N. C. Ban (2023). Considering the implications of climate-induced species range shifts in marine protected areas planning. *FACETS* 8:S2371.

Williams, S. M., and C. A. Lindell (2019). The influence of a single species on the space use of mixed-species flocks in Amazonian Peru. *Movement Ecology* 7:37.

Wilson, S., J. F. Saracco, R. Krikun, D. T. T. Flockhart, C. M. Godwin, and K. R. Foster (2018). Drivers of demographic decline across the annual cycle of a threatened migratory bird. *Scientific Reports* 8:7316.

Wilson, S., H. Lin, R. Schuster, A. M. González, C. Gómez, E. Botero-Delgadillo, N. J. Bayly, J. R. Bennett, A. D. Rodewald, P. R. Roehrdanz, and V. Ruiz Gutierrez (2022). Opportunities for the conservation of migratory birds to benefit threatened resident vertebrates in the Neotropics. *Journal of Applied Ecology* 59:653–663.

Wood, S. N. (2017). GAMs in Practice: mgcv. In *Generalized Additive Models: An Introduction with R*, 2nd edition. Chapman & Hall/CRC, Boca Raton, FL, USA. pp. 325–398.