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Prospects for Neotropical Forest Birds and Their Habitats Under Contrasting Emissions Scenarios

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ABSTRACT

Current and near future climate policy will fundamentally influence the integrity of ecological systems. The Neotropics is a region where biodiversity is notably high and precipitation regimes largely determine the ecology of most organisms. We modeled possible changes in the severity of seasonal aridity by 2100 throughout the Neotropics and used birds to illustrate the implications of contrasting climate scenarios for the region's biodiversity. Under SSP-8.5, a pessimistic and hopefully unlikely scenario, longer dry seasons ($>5\%$), and increased moisture stress are projected for about 75% of extant lowland forests throughout the entire region with impacts on 66% of the region's lowland forest avifauna, which comprises over 3000 species and about 30% of all bird species globally. Longer dry seasons are predicted to be especially significant in the Caribbean, Upper South America, and Amazonia. In contrast, under SSP-2.6—a scenario with significant climate mitigation—only about 10% of the entire region's forest area and 3% of its avifauna will be exposed to longer dry seasons. The extent of current forest cover that may plausibly function as precipitation-based climate refugia (i.e., $<5\%$ change in length of dry periods) for constituent biodiversity is over 4 times greater under SSP-2.6 than with SSP-8.5. Moreover, the proportion of currently protected areas that overlap putative refugia areas is nearly 4 times greater under SSP-2.6. Taken together, our results illustrate that climate policy will have profound outcomes for biodiversity throughout the Neotropics—even in areas where deforestation and other immediate threats are not currently in play.

1 | Introduction

Maintaining tropical ecosystems is critical to the conservation of global biodiversity, carbon storage and the survival of local peoples. Yet, forest cover continues to decline rapidly in many tropical regions (Anderegg et al. 2022; Lapola et al. 2023; Lapola, Silva, and Joly 2020). Recent analyses indicate that the ecological integrity of up to half of extant forest has been compromised by fragmentation, drought, fires, overharvesting of plants and animals, and land use such as agriculture and mining (Albert et al. 2023; Barlow et al. 2016; Grantham et al. 2020). Climate change is a cofundamental and pervasive threat to tropical forests with the potential for widespread and irreversible outcomes (Hannah et al. 2007).

Whereas increasing average temperatures and the frequency of extreme temperature events will profoundly change natural systems globally, changing precipitation regimes may present an equally or more significant direct threat to tropical forest systems (Laurance et al. 2012; Lovejoy and Nobre 2019; Phillips

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et al. 2009; Tao et al. 2022). The amount and timing of precipitation are essential to the biology of tropical systems and studies of drought in tropical forests indicate that long-term changes in rainfall regimes will lead to changes in the distribution, floristic composition, and structural complexity of tropical forests (Corlett 2016). Numerous analyses project increases in the duration and severity of dry periods in the Neotropics (Fu 2015; Tao et al. 2022) owing to likely changes in atmospheric circulation patterns (De Faria et al. 2021). Moreover, rising temperatures can lead to increased evapotranspiration, potentially exacerbating local precipitation deficits (van der Schrier et al. 2013). The dominant trend will be for more frequent and intense seasonal aridity; however, some areas such as the Pacific Andes are predicted to experience wetter conditions due to climate change (Duffy et al. 2015).

Evidence is growing that repeated exposure to moisture stress will degrade the integrity of lowland Neotropical forests, especially those classified as "moist" or "wet." These forests will likely lose their ability to recover from stress events, a change that may already be underway (Boulton, Lenton, and Boers 2022; Tao et al. 2022), and undergo wholesale change to dryer, more open forests—a process known as "savannization" (Malhi et al. 2008; Nobre and Fabrício-Neto 2021; Sales, Galetti, and Pires 2020). Severe episodic droughts have already been observed in recent decades over the Amazon basin and other regions in the Neotropics (Jiménez-Muñoz et al. 2016; Xu et al. 2011), and the tipping point for widespread changes in moist tropical forests may be soon be realized without substantial and immediate climate mitigation (Armstrong McKay et al. 2022).

For terrestrial tropical fauna, the effects of altered rainfall regimes are uncertain, but evidence is accumulating that even short-term changes in the severity of drought or seasonal aridity may significantly impact animal populations and communities in the Neotropics (Ameca y Juarez et al. 2013; Brawn et al. 2017; França et al. 2020; Ryder and Sillett 2016) and other tropical regions such as northern Australia (Chambers, Hughes, and Weston 2005), and southeast Asia (Adeney et al. 2006). A recent review developed a conceptual basis and empirical summary of the importance of precipitation to the evolutionary ecology and conservation of tropical endotherms such that dryer or wetter conditions outside of a species' "hygric niche" will impair fitness and adversely affect the viability of populations (Boyle, Shogren, and Brawn 2020). The conceptual framework of the hygric niche holds that both the quantity and timing of rainfall can affect animal survival and reproductive success.

The inevitability of climate-related environmental change has motivated interest in identifying climate refugia where ecological systems and biodiversity will be buffered and hopefully persist under predicted climate scenarios (Keppel and Wardell-Johnson 2012). Characterizing climate refugia will be particularly important for conservation priorities intended to conserve endemic species with relatively small ranges as these species are often common on islands and other geographically isolated sites (Manes et al. 2021). A related issue is the degree to which currently protected areas will suffice as climate refugia. Thus far, establishing the locations of potential refugia has focused largely on rising temperatures (Sales and Pires 2023) and projections for precipitation–moisture refugia for tropical fauna have centered on specific ecosystems and regions (Avalos and Hernández 2015; Borges and Loyola 2020; Reside, Butt, and Adams 2018; Tonetti et al. 2023).

Presented here is the first regionwide, ecosystem-based account of the potential exposure of Neotropical wildlife and extant protected areas to possible changes in rainfall regimes. We projected the severity of seasonal drought and focused on implications for the region's protected areas and birds in lowland forests—an avifauna that constitutes roughly 30% of the world's bird species (Pillay et al. 2022). Our approach was to model and contrast projections for the end of the current century under pessimistic and optimistic levels of climate mitigation.

We considered four questions under two contrasting scenarios that bracket a wide range of climate pathways (SSP-8.5 and SSP-2.6): (1) where will the duration of dry periods change throughout lowland Neotropical forests during the 21st century?; (2) what proportion of the resident forest avifauna will be exposed to changing rainfall regimes?; (3) will endemic or restricted range species be disproportionately exposed?; and (4) to what extent will currently protected areas serve as climate refugia by the end of the 21st century?

2 | Methods And Materials

2.1 | Climate Data

The historical (1970–2000) and future projection (through 2100) data for 20-year-averaged monthly precipitation are provided by the Intergovernmental Panel for Climate Change Sixth Assessment Report (IPCC-AR6), downscaled to a resolution of 2.5 arc minutes (approximately 5 km, available at https://worldclim.org/ see Fick and Hijmans 2017). The historical data used for the downscaled model outputs include databases with long-term averaged values (FAO 2001; WMO 1996), time-series of monthly averages by year (Harris et al. 2014; Lawrimore et al. 2011; Rohde et al. 2013) and daily weather data (NCEI 2015), which were all aggregated to monthly climate averages and downscaled to finer resolutions. The target temporal range for station data was between 1970 and 2000. Stations with observations for at least 25 years within this period; those with at least 10 years of data between 1960 and 2010, after removing duplicates, were considered for surface fitting. Climate data cover forested habitat at tropical latitudes between tropics of Cancer and Capricorn in the Americas at elevations from sea level to 1000 m.

The source data for future projections under the emission scenario SSP-2.6 (which represents strong sustainability efforts and a rapid transition to a low-carbon economy) and SSP-8.5 (which represents the high end of greenhouse gases emissions pathway) are from CMIP6 (the Coupled Model Intercomparison Project 6) and are calibrated based on the observed baseline climate. The result is averaged over the nine available models, including BCC-CSM2-MR (Beijing Climate Center climate system model version 2), CNRM-CM6-1 (sixth-generation atmosphere–ocean general circulation model jointly developed by Centre National de Recherches Météorologiques and Cerfacs for CMIP6), CNRM-ESM2-1 (Second generation of the Earth System Model developed by the Centre National de Recherches

Météorologiques and Cerfacs), CanESM5 (The Canadian Earth System Model version 5), GFDL-ESM4 (Geophysical Fluid Dynamics Laboratory's Earth System Model Version 4), IPSL-CM6A-LR (model developed by Institute Pierre-Simon Laplace as part of the sixth phase of the CMIP6), MIROC-ES2L (Model for Interdisciplinary Research on Climate, Earth System version-2 for Long-term simulations), MIROC6 (The sixth version of the Model for Interdisciplinary Research on Climate), and MRI-ESM2-0 (The Meteorological Research Institute Earth System Model version 2.0).

2.2 | WorldClim Data Downscaling

The monthly averages of precipitation measured at more than 47,000 weather stations globally, mostly for the 1950–2000 period, were compiled and interpolated using the thin-plate smoothing spline algorithm implemented in ANUSPLIN (Fick and Hijmans 2017), creating global climate land surfaces for monthly precipitation.

The input weather station data were collected from several sources, including The Global Historical Climate Network Dataset (GHCN), the WMO climatological normal (CLINO), the FAOCLIM 2.0 global climate database (FAO 2001), a database assembled by Peter G. Jones and collaborators at the International Center for Tropical Agriculture (CIAT) in Colombia, and some additional regional databases. The compiled database consisted of precipitation records from 47,554 locations after removing stations with errors (Hijmans et al. 2005).

The construction of the climate surfaces was done by SPLINA in the package ANUSPLIN, after dividing the global domain into 13 overlapping zones. The surface can be constructed for any specific location and elevation within the specified domain. SPLINA fits a continuous surface to the points, but the surface does not necessarily go through every observed point. The elevation data were from the Shuttle Radar Topography Mission (SRTM), and the latitude/longitude geographical coordinate system was used for all climate surfaces.

In ANUSPLIN, spline models of the observed data values are fit by setting:

$$z_i = f\left(x_i\right) + \sum_{j=1}^{p} \beta_j \varphi_j\left(x_i\right) + \varepsilon_i \; (i = 1, \cdots, n; j = 1, \cdots, p) \tag{1}$$

where f is an unknown smooth function to be estimated, the φ_j are a set of p known functions and the β_j are a set of unknown parameters which have also to be estimated (Hutchinson, 1995). The x_i commonly represent coordinates in three-dimensional Euclidean space (latitude, longitude, and elevation in this case). The ε_i are zero mean random errors. They were all aggregated to monthly climate averages after downscaled to finer resolutions. The target temporal range for station data was between 1970 and 2000.

For future projections, the first step was to estimate changes in precipitation, which were computed as the relative difference between the output of the Global Climate Models simulations for the baseline years (1960–1990) and for the target future years (2020–2100). These changes were then interpolated onto a high-resolution surface grid created, with the assumption that the change in climate does not change the spatial gradient of the climate variable that is being downscaled using Equation (1). To derive the predicted climate, the high-resolution changes were added to the high-resolution interpolated historical climate data for the baseline years.

2.3 | Calculation of Dry Season Length

We defined dry season length (DSL) as the sum of consecutive months with precipitation lower than the annual mean of monthly precipitation. To better assess the effect of rainfall regime on bird demographics, we calculated the DSL in months per year for the study area, based on the annual mean precipitation of the reference period (Li and Fu 2004; Marengo et al. 2001). The start of the dry season was marked by the change in monthly rain rate from above to below the climatological annual mean rain rate, and vice versa for defining the end of the dry season (Fu et al. 2013). This definition captures the temporal patterns of the rainfall variation to find DSL, and it is not influenced by the bias in precipitation amount in a particular dataset or model. Using the monthly precipitation provided by WorldClim, we assumed that the change of rainfall amount between adjacent months are continuous and linear. We thus determined the start (and end) of dry periods as the intercept between the precipitation timeseries and the reference annual mean. When there was more than one period in a year below annual mean, DSL is defined as the sum of their lengths. To determine predicted changes in the length of dry seasons from the present day to between 2080 and 2100, we compared predicted climate models to historical data from 1970 to 2000 and subtracted differences in DSL from the latter.

In this paper, the benchmark for "change" in the duration of DSL was 5% longer or shorter than that during the baseline period (1970–2000).

2.4 | Bird Data

The ranges of bird species were downloaded from Birdlife International in January of 2020 (Handbook of the Birds of the World and Birdlife International 2020). Using the attributes of presence and origin associated with each species' range polygons, we included only areas that were classified as extant, probably extant, or possibly extant (presence values of 1, 2, and 3, respectively), and native (origin values of 1). Additionally, we excluded range polygons classified as "non-breeding," "passage," or "uncertain" (season values of 3, 4, and 5). Of the resulting bird ranges, we removed any species where $< 50\%$ of their range overlapped with the area between the Tropic of Capricorn and Tropic of Cancer in the Caribbean and Central and South America. We filtered the remaining species to only include those species for which forest habitats are of "major" importance as defined by the habitat classification scheme in the Birdlife dataset and on the IUCN Red List. This method followed the method used by Luther et al. (2020). In addition, only year-round resident birds were included in the study; thus, austral and neotropical migrants were not included.

We utilized a global digital elevation map (DEM) with 7.5 arc-second spatial resolution to eliminate areas above 1000 m in elevation (Danielson and Gesch 2011). These areas are susceptible to large error rates in climate model outputs due to quickly changing microclimates as well as unpredictable elevation movements of avian species based on different climate scenarios. Therefore, we clipped out these areas from our climate model data and from the range areas of each species since we could not make accurate assessments of these areas.

2.5 | Data Aggregation

Data were aggregated at a scale applicable for forest restoration and management using a global grid of equal area, equal shape hexagons with a 10 km^2 resolution (Luther et al. 2020) using the R-package "dggridR" (Barnes et al. 2017). Species-specific data for the remaining species within our area of interest were spatially joined to the hexagon grid layer across their respective ranges from which we calculated the number of species in each grid cell. We also calculated the mean and median climate model projections of relative difference in DSL and dry season precipitation for each grid cell. Finally, each bioregion was joined to each grid cell using One Earth's terrestrial bioregions of the world (Dinerstein et al. 2017). We then grouped these bioregions into subregions (see Figure S1) to better represent areas with similar taxonomy and geology. To identify areas with high concentrations of area restricted endemic species (Stein, Kutner, and Adams 2000), the rarity-weighted richness (RWR) was calculated for each species as the inverse of the range size (Usher 1986; Williams et al. 1996). Specifically, RWR per hexagon $= \sum_1^n (1/c_i)$ where c_i is the number of hexagons in which species i occurs summed for the n species that occur at that hexagon. We also assessed the impact of predicted change in DSL on current protected areas using the World Database on Protected Areas (UNEP-WCMC 2020). We limited our focus to protected areas with an IUCN protected area management classification (categories I–VI). We also calculated the average and median change in the number of dry season months in each protected area to assess the impact of climate change on them (Luther et al. 2021).

3 | Results

3.1 | Predicted Changes in Rainfall Regimes

As expected, projected changes in rainfall regimes differed substantially between the SSP-2.6 and 8.5 pathways (Figure 1, Table 1). Changes of 5% or more in the duration of dry periods were predicted for 80% of lowland forest under SSP-8.5 but only 17% of the region with SSP-2.6. The extent of areas predicted to experience longer and shorter dry periods under SSP-2.6 were similar (10% and 7% of the region, respectively). In contrast, under SSP-8.5, nearly all predicted change was for dryer conditions. Extreme changes of ≥25% change in duration of dry periods were projected under SSP-8.5 for approximately 1.9 million km^2 of lowland forest (16% of the region), of which, 95% was for more severe dryness. <1% of the region was predicted to have changes ≥25% with SSP-2.6.

The extent of geographic variation in future rainfall regimes across the Neotropics differed markedly between scenarios (Table 1). Under SSP-2.6, variation over the region was comparatively modest with little change predicted for at least 70% of each subregion. Under SSP-8.5, variation among subregions was far greater and notably pervasive drying trends were projected for several areas that included nearly all Upper South America and at least 75% of the Caribbean (especially Puerto Rico), the Cerrado, the coastal Atlantic Rainforest and Amazonia (Table 1, Figure 1). Extreme increases of 25% or more in DSL were projected over 35% of Upper South America and 47% of the Caribbean with virtually no area predicted to experience shorter dry seasons within either region. Little change in the duration of dry periods was predicted under both climate scenarios for lowland forests in the South American Grasslands subregion.

In contrast to the general trend regionwide, both scenarios predicted shorter dry periods throughout much of the Andes and Pacific Coast, southern Central America (i.e., Isthmus of Panama), and western Amazonia. The two pathways predicted large-scale but opposing trends in DSL by 2100 within the western Caribbean and northern Central America (Figure 1).

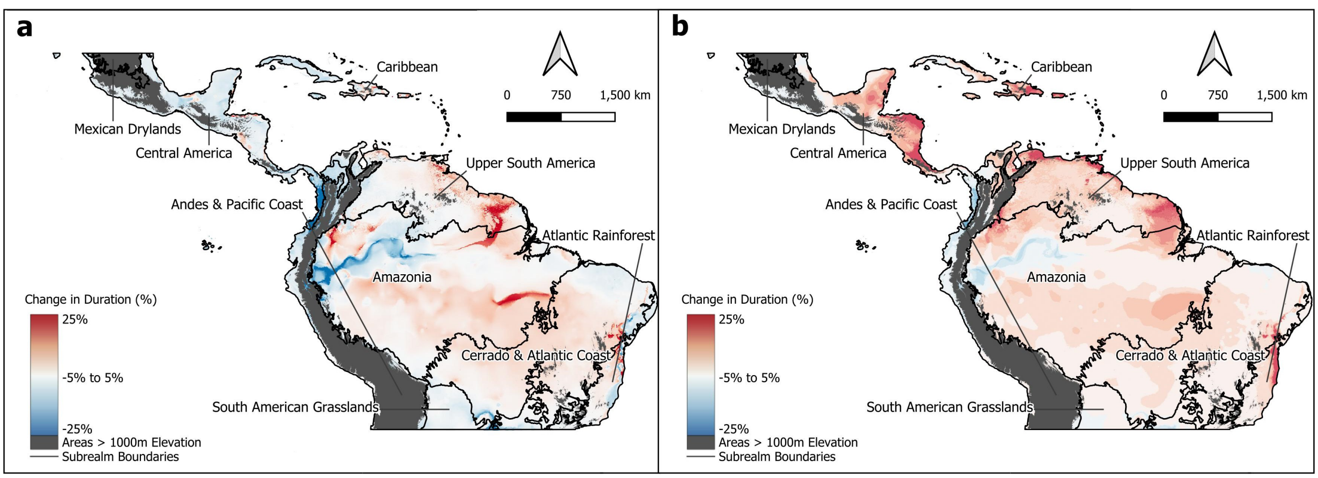

FIGURE 1 | Projected changes in the length of dry seasons by 2100 throughout the Neotropics. (A) projections under SSP-2.6; (B) projections under SSP-8.5. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

TABLE 1 | Areal extent (% of total) of projected changes in duration of dry season under SSP-2.6 and SSP-8.5 climate scenarios by the year 2100 in neotropical lowland forests.

	SSP-2.6			SSP-8.5		
Subregion and area (km^2)	**> 5% shorter**	**≤ 5% change**	**> 5% longer**	**> 5% shorter**	**≤ 5% change**	**> 5% longer**
Amazonia (5,437,866)	7%	80%	13%	5%	12%	83%
Andes Pacific Coast (488,285)	29%	70%	1%	35%	40%	25%
Atlantic Rainforest (704,152)	9%	85%	6%	4%	26%	60%
Caribbean (224,603)	< 1%	89%	11%	< 1%	11%	78%
Central America (1,084,027)	19%	78%	3%	7%	36%	57%
Cerrado (3,287,005)	2%	92%	6%	< 1%	20%	80%
Mexican Drylands (11,575)	0%	0%	0%	0%	0%	0%
South American Grasslands (358,599)	1%	99%	0%	< 1%	89%	11%
Upper South America (1,722,540)	2%	81%	17%	0%	2%	98%
TOTAL (13,292,924)	7%	83%	10%	4%	20%	76%

3.2 | Impacts of Projected Rainfall Regimes on Forest Birds

The impacts of projected changes on lowland forest birds contrasted sharply between the two pathways throughout the Neotropics (Figure 2, Table 2). Under SSP-2.6, only 84 species (< 3% of the entire region's avifauna) may experience dryer conditions, but 748 species are predicted to face shorter dry periods—over twice that expected under SSP-8.5. In contrast, under SSP-8.5, 2444 (79%) of the region's lowland forest bird species, and over 20% of the world's avifauna, will potentially be exposed to altered rainfall regimes by 2100; of these, 2097 species were predicted to face longer dry periods and 347 will be exposed to shorter periods.

Contrasts in the possible consequences of the two climate scenarios for resident avifaunas were especially evident within certain subregions (Table 2, Table S2). For example, the number of species potentially exposed to altered rainfall regimes increased over tenfold between pathways in the Caribbean, Cerrado, and Upper South America subregions. In Amazonia, more than 1000 species are predicted to face potentially dryer conditions under the SSP-8.5 pathway; only 19 species are predicted to experience longer DSL with SSP-2.6. The Andes Pacific Coast and Mexican Drylands regions were exceptional as no species were projected to face dryer conditions under SSP-2.6 but a large proportion of the resident avifaunas are expected experience more severe seasonal aridity under SSP-8.5.

Under SSP-8.5, over half of the area-restricted endemic species are predicted to face longer dry seasons (Figure 2, Table 2). For the Caribbean, where 80% of the total resident avifauna is endemic to the region, nearly all species (96%) will be exposed to greater DSL. Longer dry seasons are predicted for all area-restricted endemic species (N = 107) in Upper South America. Other subregions where notably large proportions of endemics may be heavily impacted under SSP-8.5 include the Amazon, and Central America (Table 2). With SSP-2.6, only 84 (6.6%) of the area-restricted endemics for the entire Neotropics are projected to face > 5% longer dry seasons, of which, 53 are in the Caribbean. Notably, 262 (58%) of the endemic species in the Andes Pacific Coast will face substantially shorter dry seasons under the SSP-2.6 scenario.

3.3 | Impacts of Projected Rainfall Regimes on Climate Refugia and Extant Protected Areas

The two pathways also presented distinctive scenarios for the extent of potential climat refugia in the Neotropics by 2100 (Figure 3). Defining refugia broadly as areas where DSL will stay within ± 5% of the 20th-century baseline, we found that only 19% of the lowland Neotropics will encompass potential refugia areas under SSP-8.5. By contrast, nearly 84% of the entire region will potentially constitute refugia areas according to SSP-2.6—a difference of approximately 8,400,000 km^2. Differences between pathways in the extent of potential refugia were most evident for Amazonian, Caribbean, Cerrado and Atlantic Coast, and Upper South America subregions. Consequences for Upper South America were especially severe as only 2% of the entire region will provide climate refugia according to SSP-8.5, but 81% of the region will qualify under SSP-2.6. We found similar differences for Amazonia where 79% and 12% of the lowland forests will function as refugia under SSP-2.6 and SSP-8.5, respectively.

Projected changes in DSL also revealed significant implications for the integrity and lasting value of current protected areas as future reserves for birds and overall biodiversity (Figure 4, Table S1, Figure S2). At present, there are 3105 protected areas in the lowland Neotropics (UNEP-WCMC 2020). Of these, 66% (N = 2060) will lie completely outside the regions projected as climate refugia under SSP-8.5 compared to only 8% of the current protected areas under the SSP-2.6 forecasts (Figure 4, Tables S1 and S3). In terms of overall area, 94%

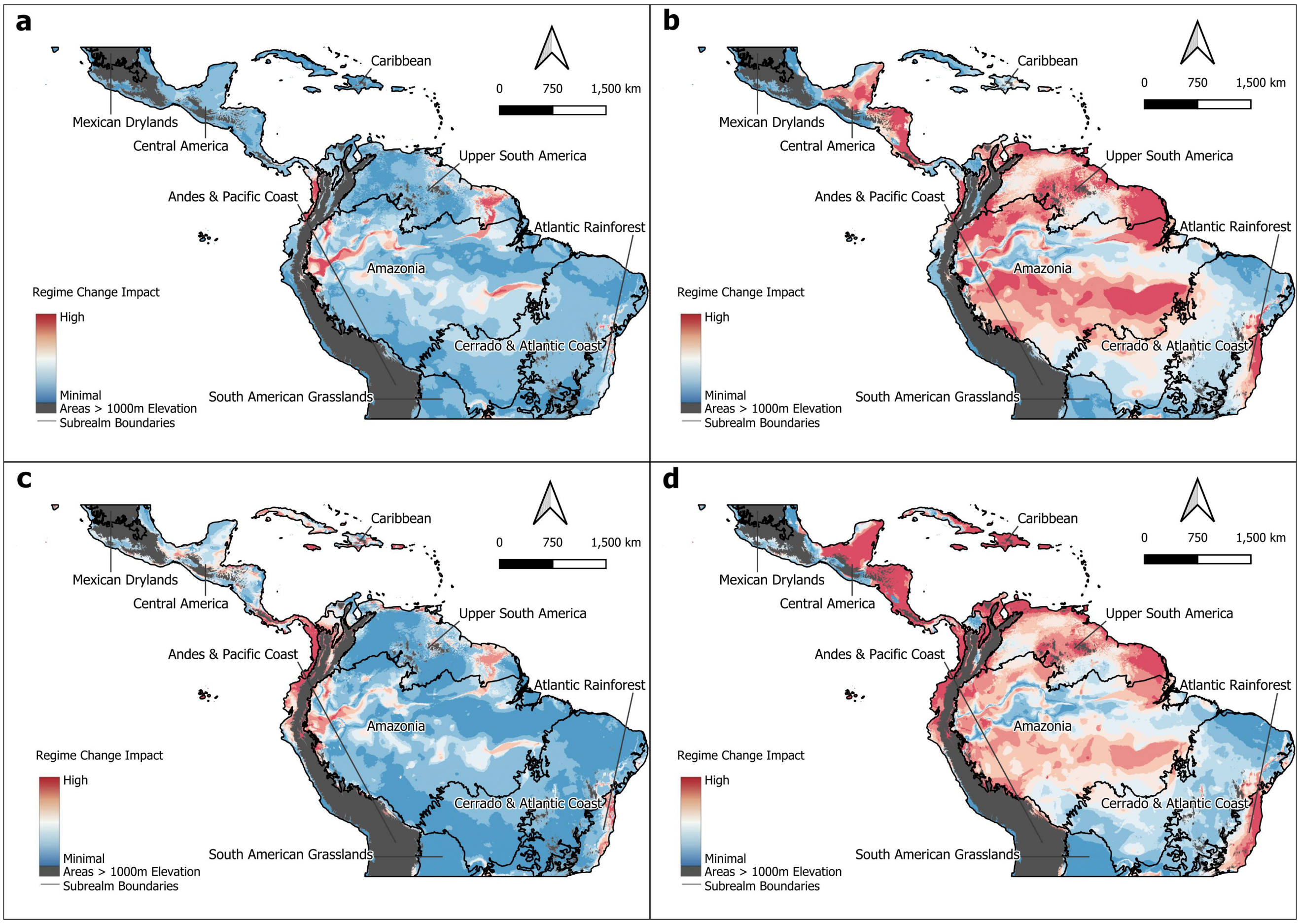

FIGURE 2 | Exposure of Neotropical lowland birds to projected changes in length of dry season. The color codes represent both the number of bird species and the magnitude of the predicted change in dry season length. Thus, locations predicted to have higher precipitation regime change impact by the year 2100 have both a greater number of species and a larger change in dry season length. (A) all species under SSP-2.6 projections; (B) all species under SSP-8.5 projections; (C) area-restricted endemic species under SSP-2.6; (D) area-restricted endemic species under SSP-8.5. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

and 22% of the current protected areas will lie in projected refugia under SSP-2.6 and SSP-8.5, respectively. The magnitude of differences between forecast scenarios varied among subregions with the Caribbean, Upper South America, and Amazonia having the greatest difference between the proportion of protected areas in refugia areas and the Andes Pacific Coast the least difference between the two scenarios. For the Caribbean, by 2100 barely 1000 km^2 (11%) of currently protected areas will overlap with projected climate refugia under SSP-8.5 (Table S1).

4 | Discussion

Our analyses under optimistic and pessimistic scenarios demonstrate that the magnitude of climate change through the 21st century will have profound implications for the sustainability of neotropical forests and their constituent animal biodiversity. Although this is not a novel finding, our study constitutes the first regionwide precipitation analysis for the Neotropics' lowland-forest birds and existing protected areas. Unmitigated climate change may lead to altered precipitation regimes in the 21st century that could compromise the integrity of lowland forests on a regionwide basis throughout the Neotropics. If realized, these changes will affect a large proportion of extant protected areas and limit the availability of putative climate refugia for lowland biodiversity, as illustrated here for forest birds. The level of threat will be especially severe—possibly catastrophic—in the Caribbean, Upper South America, and southern Amazonia regions. A future with comparatively modest climate change, while challenging, bodes comparatively well for a large proportion of extant protected areas and provides far better availability of climate refugia. The Andes Pacific Coast subregion is an exception, as both scenarios project widespread and wetter rainfall regimes.

Direct habitat loss and degradation are currently the most pervasive threats to neotropical forests (Albert et al. 2023; Lapola et al. 2023); nonetheless, the severity of climate change will be critical to the long-term success of measures intended to ensure the conservation of the world's most diverse avifauna and perpetuation of neotropical lowland forests. Whereas our analyses have focused on precipitation, rising temperatures will also present a climate-related threat to the sustainability of tropical forests. Warming trends and novel temperature regimes have been observed throughout most of the world's tropical

TABLE 2 | Numbers of neotropical bird species potentially affected by projected changes in duration of dry season under SSP-2.6 and SSP-8.5 through the year 2100. For subregions, the top row of numbers is the total number of species found in that subregion; the row below is that number of area-restricted endemic species unique to that region.

	SSP-2.6			SSP-8.5		
Area	**> 5% shorter**	**< 5% change**	**> 5% longer**	**> 5% shorter**	**< 5% Change**	**> 5% longer**
Amazonia						
1604	347	1238	19	60	231	1313
142	8	132	2	1	12	129
Andes Pacific Coast						
1882	679	1203	0	324	306	1252
453	262	191	0	213	130	110
Atlantic Rainforest						
660	1	654	5	2	77	581
55	1	51	3	2	7	46
Caribbean						
224	4	166	54	0	7	217
179	4	122	53	0	6	173
Central America						
1187	473	713	1	155	209	823
329	64	265	0	5	68	256
Cerrado and Atlantic Coast						
958	7	948	3	4	94	860
16	0	16	0	0	2	14
Mexican Drylands						
241	7	234	0	0	71	170
2	0	2	0	0	2	0
South American Grasslands						
488	26	462	0	7	70	411
0	—	—	—	—	—	—
Upper South America						
1213	240	950	23	12	76	1125
107	0	98	9	0	0	107
Overall Neotropics						
3115	748	2284	84	378	680	2097

forests and extend from the forest canopy down to the understory (Trew et al. 2024) and recent analyses indicate that temperature increases expected under pessimistic climate scenarios (i.e., SSP-6.0–8.5) may push tropical tree species to physiological thresholds beyond which their photosynthetic function may be compromised (Doughty et al. 2023). The added or interactive effects of rising temperatures with changes in rainfall will challenge tropical fauna as well. Whereas the thermal ecology of tropical birds and the environmental limits within which these species can maintain homeostasis merits much study (Pollock et al. 2021; Pollock et al. 2024), behavioral thermoregulation in several understory bird species appear to be driven by local temperatures, rainfall, and local humidity (Jirinec 2024). Our projections are independent of ongoing threats to forest bird habitat posed by deforestation, fires, and local land use and reports indicate that the pace of these threats is more rapid than those directly attributable to current climate change (Albert et al. 2023). Importantly, deforestation appears to exacerbate climate-based moisture stress in forests at local and possibly regional spatial scales owing to decreased evapotranspiration and

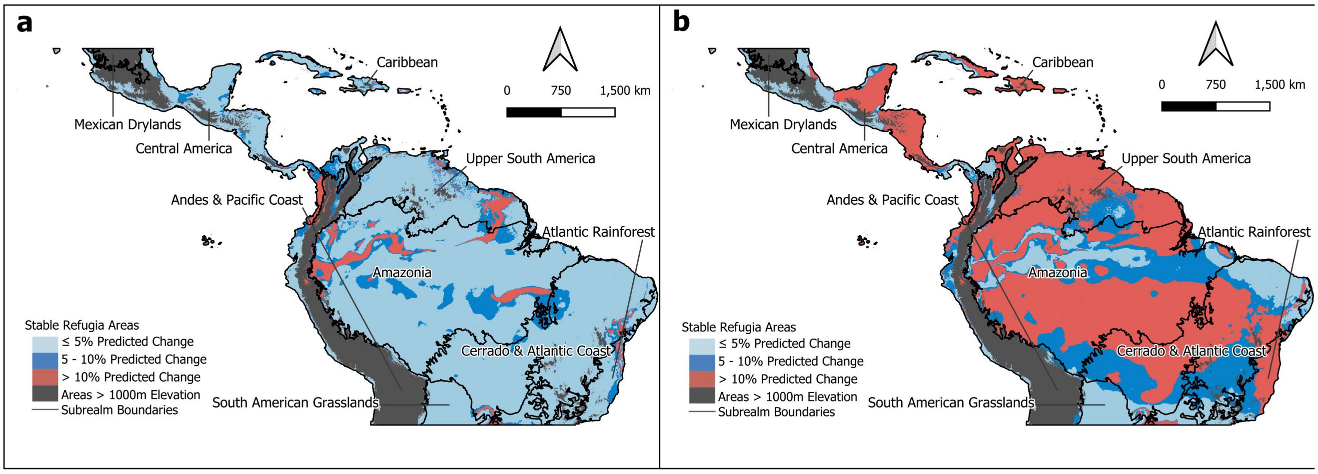

FIGURE 3 | Potential climate refugia zones. (A) refugia under SSP-2.6 projections; (B) refugia under SSP-8.5 projections. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

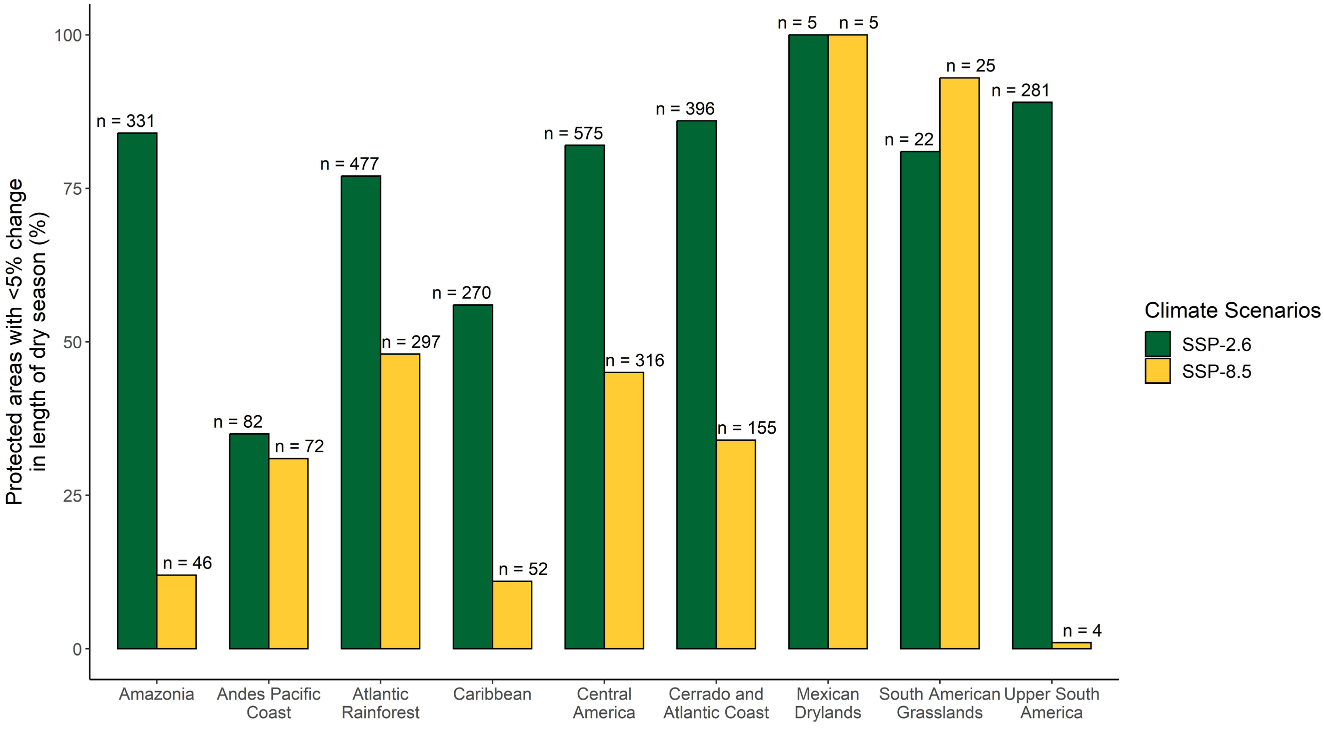

FIGURE 4 | The percent of protected areas in a subregion with predictions of < 5% change in the length of the dry season by the year 2100 under SSP-2.6 (green) and SSP-8.5 (yellow) projections. Higher values indicate a greater proportion of protected areas in a subregion with relatively stable precipitation regime projections. N equals the number of protected areas that will have a < 5% change in the length of the dry season in the subregion.

increased runoff (Aragão 2012; Lawrence and Vandecar 2015; Staal et al. 2015). Significantly dryer conditions owing to feedbacks between land use and local moisture availability have been well-documented in southern Amazonia (Coe et al. 2013). Moreover, recent work linking deforestation and fire to rainfall indicate that forest loss can exacerbate local moisture stress and may push Amazonia closer to a critical threshold beyond which the entire subregion's seasonal rainfall patterns will be disrupted (Bochow and Boers 2023). Deforestation may therefore lead to local and regional changes in precipitation regimes at velocities exceeding those predicted here even under the more pessimistic climate scenario (Feeley et al. 2012).

Increases in aridity over the long-term are predicted to push lowland forests toward open savanna-like habitat, a change that will cause substantial changes in constituent forest bird communities. Even comparatively short-term episodes of intense seasonal aridity, such as those associated with ENSO events, appear to decrease the productivity of lowland forests and negatively affect the reproductive behavior and breeding success of several neotropical bird species and other wildlife (Brawn et al. 2017; Martin and Mouton 2020; Sales, Galetti, and Pires 2020). Less clear is the fate of ecosystems and wildlife populations in areas such as the Andes Pacific Coast that may experience less severe seasonal drought; however, there is evidence that significantly more rain can also have adverse outcomes for lowland forest birds and change the structure of historically dryer forests (Boyle et al. 2020; Takano-Rojas et al. 2023).

Whereas the mechanisms underlying the responses of neotropical bird populations to episodic drought require study, dryer conditions will likely affect the availability of food resources; which, for most neotropical bird species, consists of some combination of arthropods, fruit, and nectar (Stutchbury and Morton 2022). Episodic drought can have a positive effect on fruit and nectar production (Skutch 1950; Wright et al. 1999), but longer-term drought will lead to loss of forest resiliency and reproductive failure. Outbreaks of arthropods such as certain Lepidopterans can follow episodes of intense aridity (Van Bael et al. 2004); however, experimental evidence indicates that lasting dry conditions will decrease overall arthropod abundances in humid forests (Gely et al. 2020). Trend estimates for tropical arthropods from long-term studies in Costa Rica and elsewhere suggest that regional declines in the abundances of selected arthropod groups are partly attributable to reductions in rainfall that have already been realized (Janzen and Hallwachs 2021).

Far more research is needed to estimate the thresholds for change in precipitation regimes beyond which the viability of tropical bird populations and overall integrity of lowland forest ecosystems will be compromised. Our modeling adopted a threshold of 5% for "change" but whether this benchmark is realistic requires continued study. How individual species will react to altered rainfall regimes and associated habitat changes is difficult to predict, as vulnerability to changing environments may be a complex function of intrinsic traits and ecological interactions (Beissinger and Riddell 2021). Recent analyses indicate that species' traits can have limited value in predicting the fates of individual species facing environmental change (Wiethase et al. 2024). Thus, field-oriented monitoring programs will be needed to assess and predict the relative vulnerability of species as climatic conditions change.

Whereas a wide spectrum of reactions among species is likely—empirical evidence confirms that understory forest birds in general, and area-restricted endemic species in particular, are highly sensitive to environmental change owing to low vagility (Manes et al. 2021; Moore et al. 2008). Many species of terrestrial and understory insectivores, for example, appear unable to disperse over open habitat or persist in highly altered, open forests (Powell et al. 2015). Limited vagility may restrict the ability of many lowland forest species to extend their ranges to more climatically favorable areas. For many areas, the geographic extent of projected changes in rainfall regimes is so extensive that many lowland species may simply have "no place to go"—even within intact tracts of forest. We do not contend that all species exposed to changing rainfall regimes will be adversely affected—some species will certainly benefit. Nonetheless, we concur with previous analyses that predict "many losers and few winners" for tropical fauna under plausible climate change scenarios and continued deforestation (Tabarelli et al. 2012).

Protected areas are fundamental to the sustainability of tropical biodiversity and, whereas their success appears to vary among taxa (Fajardo et al. 2023), protected sites have already proven effective in conserving endemic and threatened species of birds in the Neotropics (Cazalis et al. 2020) and around the world (Bolam et al. 2021; Luther et al. 2021). Our results and other reports (Torres-Amaral et al. 2023) show that the continued value of many protected areas in the Neotropics may be undermined by significant changes in precipitation regimes. Planning for future protection should therefore take climate change forecasts into account and identify potential climate refugia that will plausibly protect neotropical biodiversity in the 22nd century. Climate refugia will be especially valuable if they can be protected from the land use changes that are ongoing throughout the Neotropics (Hansen et al. 2020). Policy guidelines for sustaining tropical biodiversity under different climate scenarios have been presented and suggest that with $\leq 2°C$ change, protecting 30% of tropical terrestrial landcover will reduce extinction risks (all taxa) by 50% (Hannah et al. 2020). Finer spatial scale analyses than those presented here will be needed to identify the locations and extent of potential climate refugia regarding expected change in rainfall. For example, local floodplain areas may offer microclimate refuge in otherwise dry areas. We hope our analyses will add to the ongoing dialog about where future protected areas need to be established or maintained for birds and other components of tropical biodiversity, especially under pessimistic scenarios and in regions where changes in precipitation regimes may be widespread and severe.

Author Contributions

Jeffrey D. Brawn: conceptualization, methodology, project administration, supervision, validation, visualization, writing – original draft, writing – review and editing. **David Luther:** conceptualization, formal analysis, methodology, supervision, validation, visualization, writing – original draft. **Mingxin Qu:** conceptualization, formal analysis, methodology, validation, writing – review and editing. **Sarah M. Farinelli:** formal analysis, methodology, validation, visualization, writing – review and editing. **W. Justin Cooper:** formal analysis, methodology, validation, visualization, writing – review and editing. **Rong Fu:** conceptualization, formal analysis, methodology, supervision, writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in Dryad at https://doi.org/10.5061/dryad.h9w0vt4sm and in Zenodo at https://doi.org/10.5281/zenodo.13883438.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.