



Future climate change will impact the migration of New World migrant flycatchers (Tyrannidae)

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Abstract

Climate change is reaching several tipping points, likely resulting in habitat shifts at a global scale. Such changes could have serious consequences for migratory species. For instance, climatic changes may impact the distribution of breeding and non-breeding ranges, resulting in longer migration distances for some species. The flycatchers (Tyrannidae) are the largest family of birds in New World. They are small insectivorous birds with different distributions and migratory strategies, including both tropical and temperate species. Here, we aim to map the climatically suitable ranges for Tyrannidae in the future, compare them to their present ranges, and quantify the changes in range size and in migratory distance. We show different impacts on species that breed in the northern vs. southern hemisphere. Furthermore, results suggest that tropical and temperate species would suffer from different stressors. Neotropical austral migrant species would lose part of their breeding ranges, while Nearctic–Neotropical species would need to fly longer distances to reach the same climatic conditions of their current breeding ranges. Because past climate shifts have shaped the evolution of bird migration, these insights are also key for elucidating the mechanisms underlying the evolution and regulation of bird migration, and for conservation planning.

Keywords BioClim · Intra-tropical · Migratory systems · Nearctic–Neotropical · Neotropical austral · Species distribution models

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Introduction

Organisms are currently responding to climate change by shifting their distributions or adapting their behavior/physiology (Huntley et al. 2006; Cox 2010). Global temperatures are rising more rapidly now than in the last 65,000 years (Diffenbaugh and Field 2013), and predictions estimate global temperature increases of 1.4 to 4.4°C at the end of the twenty-first century (IPCC 2021). Not surprisingly, bird migration patterns across the planet are changing (Rushing et al. 2020). Many effects have already been registered, such as a decrease in migratory activity (Pulido and Berthold 2010), changes in the latitude of non-breeding and breeding ranges (Brommer 2004; Fiedler et al. 2004; La Sorte and Thompson-III 2007), phenological mismatches between timing of bird movements and resource peaks (Shiple et al. 57), decreases in migration distance for short-distance migrants (Visser et al. 63), and advances in the timing of breeding and spring migration (Usui et al. 60; Samplonius et al. 2018; Shiple et al. 57). Thus, migratory birds that depend on conditions that are hundreds to thousands of kilometers distant

during different parts of their annual cycle face a complex set of challenges under ongoing climate change.

Migration is a complex life history strategy used by many birds in response to seasonality (reviewed by Berthold 1996). In the New World, major avian migratory systems are (1) Nearctic-Neotropical migration, in which birds breed at north-temperate latitudes and overwinter in the Neotropics; (2) Neotropical austral migration, in which birds breed at south-temperate latitudes and migrate northwards to overwinter closer to the equator; and (3) Intra-tropical migration, in which birds breed and migrate completely within the tropics. Regardless of where they migrate, the migratory patterns of all of these species are molded by climate, continent shape, and topography (Chesser 1994; Dingle 2008; Jahn et al. 2020). Thus, some general patterns are evident. For example, migratory distances are longer for Nearctic-Neotropical migrants than for other New World migrants, and breeding ranges are smaller for Neotropical austral migrants than for species in other migratory systems (Jahn et al. 2004; Faaborg et al. 2010).

Migratory birds rely on using a specific series of locations throughout their annual cycle, often located in regions that cross political borders (Valente et al. 61; Grecian et al. 2012), and which may change over time (Milá et al. 2006). Thus, mapping the general impacts of the ongoing climate change for migratory birds is an important tool for exploring and planning effective conservation strategies to improve an international network of protected locations (e.g., Runge et al. 2015). Furthermore, because past climate shifts have substantially molded the evolution of bird migration (Milá et al. 2006), these insights are also key for elucidating the mechanisms underlying the evolution and regulation of bird migration.

Here, we aim to map the future distribution that New World birds might have if they are able to track their current climatic requirements. We then quantify their new breeding, non-breeding, and permanent residence ranges, and the migratory distances between them. We focused on New World flycatchers (Tyrannidae; hereafter, “flycatchers”), the largest New World bird family, species of which inhabit most ecosystems (Chesser 1994; Rappole 1995; Parker et al. 1996), present a high diversity of migratory systems and breed across most latitudes in the New World. Therefore, they represent an ideal model for understanding the potential impacts of climate change on migratory birds at a continental scale across the Americas.

Our hypothesis is that birds in different migratory systems face different risks due to the combined effects of climate change and geography. We expect that, under future climate change, (1) species in the Nearctic-Neotropical migratory system will track climate changes, following the observed trend for many birds in North America to move northward (La Sorte and Thompson-III 2007; Rushing et al. 2020) and,

as a consequence, will experience an increase in the distance between breeding and non-breeding ranges, and that (2) species in the Neotropical austral migratory system will face a decrease in the size of their breeding ranges, as a consequence of the combination of climate change (which will push species southwards) and the shape of South America, which increasingly narrows southwards (Chesser 1994; Hawkins and Diniz-Filho 2006). Thus, the available breeding area for those birds should be smaller in the near future.

Methods

Bird distribution data

Flycatcher species distributions were obtained from digital bird distribution maps available from BirdLife International and Handbook of the Birds of the World database (hereafter, “BL–HBW”) (BirdLife International and Handbook of the Birds of the World 2018). Tyrannidae comprise 450 species (HBW and BirdLife International 2018), which includes approximately 32 Nearctic-Neotropical migrant species (Rappole 1995) and 76 Neotropical austral migrant species (representing approximately one third of the species in this system) (Chesser 1994; Cueto and Jahn 2008). As defined by BL–HBW, these maps were derived from specimen localities (from museum data), records for species in the Global Biodiversity Information Facility, observer records from BirdLife International’s Red Data Books, distribution maps in field guides and other handbooks, expert opinion, and other sources that were reviewed by BL–HBW. The complete set of references of distribution data is available in the Metadata section of BirdLife International and Handbook of the Birds of the World (2018).

We assigned species to a migratory system based on the polygons in the BL–HBW database, then corroborated this classification using publications on specific migratory flycatcher species (supplementary material Table S1). Thus, we selected 29 Nearctic-Neotropical, 11 Intra-tropical, and 40 Neotropical austral migrant flycatcher species for analysis. We did not include altitudinal migrants (i.e., species with seasonal breeding and non-breeding ranges at different elevations in mountainous regions), even though some flycatchers are known to be altitudinal migrants in the Neotropics (Barçante et al. 2017), because data on their seasonal distributions are lacking.

Inclusion of each phase of the annual cycle, with different climatic restrictions, is key to evaluate impacts on migratory birds (Doswald et al. 2009; Wilson et al. 65; James and Abbott 2014; Ponti et al. 2020). We therefore divided polygons into breeding, non-breeding, and permanent residence ranges, encoded according to BirdLife International and Handbook of the Birds of the World (2018), to evaluate the

effects of climate change on each stage of their annual cycle and on the migratory movements between these ranges. Notably, approximately 10% of flycatcher species are partial migrants (Dufour et al. 2020), i.e., species with individuals that migrate and other individuals that do not migrate (Jahn et al. 2010; Dufour et al. 2020). Thus, permanent residence ranges are considered to be those in which at least part of the population remains resident throughout the year, even though part of that population—often younger individuals—may migrate (Jahn et al. 2010).

Climate variables and species distribution models

Species distribution models were built separately for each oceanic-atmospheric circulation model (AOGCM). First, we separated breeding, non-breeding, and resident ranges, with their different climatic conditions, aiming to evaluate impacts on the different types of ranges in the near future (Doswald et al. 2009; Wilson et al. 65; James and Abbott 2014; Ponti et al. 2020). We modeled climatic conditions for each range separately, assuming that habitat requirements for the breeding, non-breeding, and permanent resident ranges are defined by general climatic conditions. This means that if a species selects a certain range during the summer for breeding, it is constrained not only by summer climatic conditions, but also by its winter conditions, which, together, will define the type of ecosystem and resources (food) that it will select. We modeled the extreme climate scenarios, the RCP 2.6 and the RCP 8.5 (Representative Concentration Pathways). As the current course of climate change is closer to the predictions of RCP 8.5 (IPCC 2014; Christensen et al. 2018), we have decided to present these results. The results of RCP 2.6 are available in the Online Resource section. We outlined the details of climate variables and species distribution models in Fig. 1.

We used climatic simulations from the 5th phase of the Climate Model Intercomparison Project (CMIP5) (Taylor et al. 58). We downloaded the CMIP5 data at a 0.5° spatial resolution, available at ecoclimate.org (Lima-Ribeiro et al. 2015). In all our models, we used four temperature variables (annual mean temperature, seasonality, maximum temperature of the warmest month, minimum temperature of the coldest month: BIO 1, 4, 5, 6), and four precipitation variables (annual precipitation, precipitation of the wettest month, precipitation of the driest month, seasonality: BIO12, 13, 14, 15), aiming to define general habitat conditions throughout the annual cycle. Among the global models of oceanic-atmospheric circulation (AOGCMs), we used six that have projections for two extreme future scenarios, RCP 2.6 and RCP 8.5, namely, CCSM, FGOALS, GISS, IPSL, MIROC, and MRI. For the current period, we used simulations of the variables from 1950–1999, and for future simulations we used the years 2080–2100 (Taylor et al. 58).

Our distribution models were generated using the BioClim method (Busby 1990) (bioclim function (dismo package (Hijmans et al. 2014))). First, we extracted climate data for all species polygons and subsequently eliminated climatic outliers for each species. The Bioclim model is very sensitive to outliers, in our case, presence points with extreme/unique climatic conditions (Varela et al. 62). Presence-absence maps were built using continuous output (percentile distribution of the data), cutting it with a species-specific threshold (“optimize” function [package stats (R Core Team 2019)]). The species-specific threshold was the result of minimizing the sum of the commission and omission errors. The commission errors were quantified in relation to the size of the model area, not in relation to the number of points used in all analyses, which can underestimate errors at continental/large scales when using metrics such as true skill statistics (TSS) or area under the curve (AUC), as in Eq. (1).

$$\text{Commission error} = \frac{b}{a + b} \quad (1)$$

where a = true positive, b = false positive, and $a + b$ = model area. Thus, the false positive rate was not underestimated due to the large validation area (i.e., the New World) relative to the size of species distribution areas. This allowed us to calculate the proportion of the model that is incorrect.

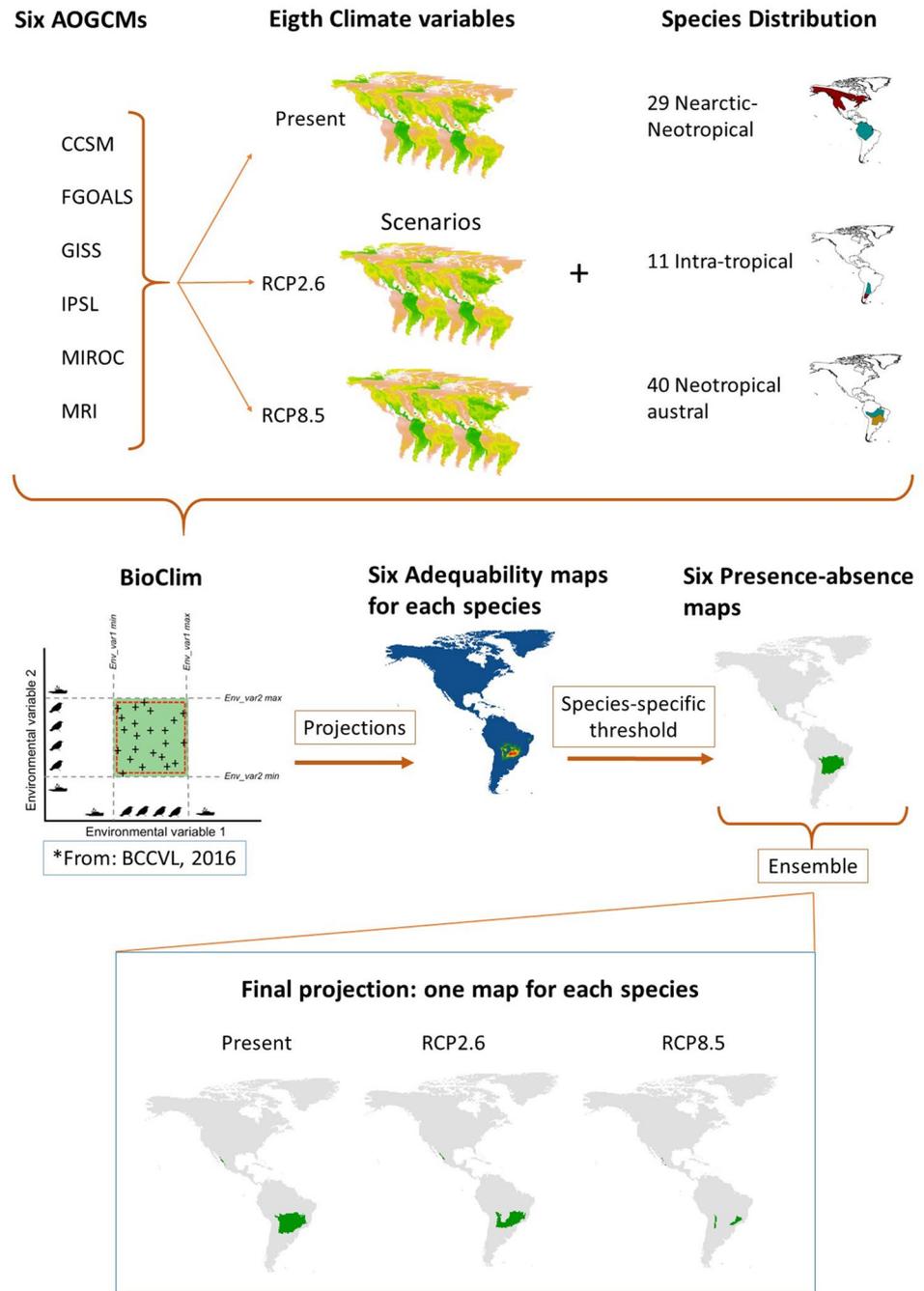
The breeding ranges were projected separately in each hemisphere, that is, Neotropical austral migrant breeding ranges were projected onto South America, Nearctic-Neotropical migrant breeding ranges were projected onto North and Central America, and Intra-tropical migrant breeding ranges were projected across the Neotropics. This is because climatic conditions could look similar in the north vs. southern hemisphere, but the changes in breeding ranges would be unrealistic.

Finally, we generated consensus projections (ensembles) from ranges where at least three climate models overlapped (Araújo and New 2007; Diniz-Filho et al. 2009). To evaluate the raw and the consensus models, we calculated sensitivity and commission values. This methodological process is shown in Fig. 1.

Data analysis

From ensemble maps, we obtained all measures for data analyses. We quantified centroid points and total area (km²) for breeding, non-breeding, and permanent residence ranges for current and future predicted distributions. We also obtained species richness maps across the New World. We evaluated changes in the centroid location in two ways: (1) the direction in which the displacement was projected, and (2) the distance of its future location from the present location. The

Fig. 1 Details of climate variables and species distribution models for 80 Tyrannidae species (flycatchers) under the high emissions scenario (RCP 8.5)



Biodiversity and Climate Change Virtual Laboratory (BCCVL), 2016. Bioclim [WWW Document]. URL <https://support.bccvl.org.au/support/solutions/articles/6000083201-bioclim> (accessed 5.7.21).

direction of centroid movement was calculated using the `gzAzimuth` function (`maptools` package (Bivand and Lewin-Koh 2015)). We then tested whether there was any directional trend of centroid displacement in each migratory system (Rayleigh uniformity test (Jammalamadaka and SenGupta 2001), using the `rayleigh.test` function (`circular` package (Agostinelli and Lund 2013))).

The distance between the present and future centroids was calculated using the “`distVincentyEllipsoid`” function (`geosphere` package (Hijmans 2014)). Centroid displacement distance was used as a response variable in a set of candidate linear models: (1) null model = a fixed intercept at zero, representing no centroid displacement; (2) climate = accounting for the effects of climate change through a fixed intercept, regardless of migratory system; and (3)

climate and system = accounting for the effects of climate change on centroid displacements differently for each migratory system.

To evaluate how the size of areas (km²) (area function (raster package (Hijmans 2019))) and migration distances between pairs of modeled occurrence ranges (distVincentyEllipsoid function) are affected by migratory system and climate change, we independently built, for each of these response variables, a set of five candidate mixed models, using species as a random factor in all cases and different combinations of mixed factors: (1) null model = using only a fixed intercept, representing the absence of changes in the size of areas/migratory distances; (2) climate = a comparison between climatic periods (present and future); (3) system = a comparison between migratory systems; (4) climate + system = an additive association of models, comparing climatic periods by migratory system; and (5) climate × system = the interaction of the models, comparing climatic periods by migratory system. For area size, we used generalized linear mixed models, with a Gaussian error distribution and log link, while for migration distances we used linear mixed models. The candidate models were selected using the Akaike information criterion (AIC) (Burnham and Anderson 2002). We considered the models within two points of AIC as equally ranked, and within those always selected the ones with the lowest number of parameters.

The combination of different changes in the size of breeding, non-breeding, and permanent residence ranges, their locations, and migratory distances allowed us to identify trends in geographic distribution and migratory movements within each migratory system. All data processing, models, and analysis were done in the R environment (R Core Team 2019). The scripts and data are available at <https://github.com/IsaBraga/bird-migration-and-climate-change>.

Results

In general, we observed a tendency for species to lose climatically suitable ranges throughout their annual cycle in all migratory systems, with distinct differences between them. In addition, six species (one Neotropical austral, three Nearctic-Neotropical, and two Intra-tropical migrant species) could become extinct as a result of losing their entire range (Table 1). Changes in migration distance varied according to migratory system, with all Nearctic-Neotropical migrant species increasing the distances between breeding and non-breeding ranges, which did not occur in the Neotropical austral migratory system.

Results of both RCPs exhibit similar trends, although RCP 2.6 results are less extreme, predicting fewer extinctions (results from RCP 2.6 are available in the supplementary material). The modeled ranges of some non-breeding ($n = 4$) and permanent residence ranges ($n = 1$) were removed from the analysis because the resulting distribution was considered unrealistic. For example, the predicted non-breeding range of *Myiarchus cinerascens* which is currently located in Central America, was predicted for the Brazilian Atlantic Forest and induced very high variation in the models.

Regarding the quality of models, sensitivity values were high for most species (mean ± SD = 0.74 ± 0.14) and did not vary between breeding, non-breeding, and permanent residence ranges (supplementary material Table S2). On average, model sensitivity improved by 15% when the ensemble of all six climate models was used. We obtained low commission values (mean ± SD = 0.27 ± 0.15) that also improved with the use of model ensemble (mean ± SD = 0.21 ± 0.19). For breeding ranges, commission decreased by 20%, and for non-breeding and permanent residence ranges, reduction in over-prediction was 24% and 17%, respectively,

Table 1 Number of migratory New World flycatchers (Tyrannidae) species according to number of ranges currently occupied, number of ranges reduced to zero in the future (lost full range), only one remain-

ing range, and no ranges remaining under the high emissions scenario (RCP 8.5), by migratory system

Ranges			Migratory systems			Total
			Nearctic-Neotropical ($n = 29$)	Intra-tropical ($n = 11$)	Neotropical austral ($n = 40$)	
Breeding	Currently occupied		29	5	23	57
	Future	Lost full range	8	3	5	16 (28%)
		Only one remaining range	5	0	1	6 (10%)
Non-breeding	Currently occupied		24	9	38	71
	Future	Lost full range	8	5	11	24 (34%)
		Only one remaining range	0	2	1	3 (4%)
Permanent residence	Currently occupied		14	10	27	51
	Future	Lost full range	8	5	2	15 (29%)
		Only one remaining range	5	4	7	16 (31%)
Lost all future ranges			3	2	1	6

when the ensemble was used (supplementary material Table S2).

Changes in size of areas

Results show that about one-third of species may completely lose one of their climatically appropriate breeding, non-breeding, or permanent residence ranges in the future (Table 1). Another 16 species are predicted to lose their breeding and non-breeding ranges, remaining only in the range of permanent residence (seven Neotropical austral, five Nearctic-Neotropical, and four intra-tropical migrant species) (Table 1). In general, species with small ranges (smaller than 170,000 km², i.e., smaller than the country of Surinam) would suffer high impacts from climatic change. Specifically, the climatic conditions of their current breeding ranges are predicted to disappear in the near future. Further, six species would not have any climatically suitable areas in the future (breeding, non-breeding, and/or permanent residence ranges) and may become extinct if they are not able to adapt to the new conditions (Table 1).

Present-day breeding range size was significantly different between migratory systems, with those of Nearctic-Neotropical migrants being 2.5 times larger than those of Neotropical austral migrants ($z = -2524.87$, $p < 0.0001$), and four times larger than those of intra-tropical migrants ($z = -2183.45$, $p < 0.0001$) (interaction model in mixed model selection, supplementary material Table S3). This difference is expected to double in the future. The projected losses in breeding ranges differed between migratory systems, being 340,000 km² on average for Neotropical austral migrant species (60%) and 180,000 km² for Nearctic-Neotropical migrant species (12%) (Fig. 2).

There were differences in the size of non-breeding ranges only between the present and future, not between the migratory systems, with larger predicted losses than for breeding ranges, which is a similar pattern across all migratory systems (Fig. 2). Non-breeding ranges are expected to be reduced by almost 810,000 km², on average (82%) (climate model in mixed model selection, supplementary material Table S3).

Changes in permanent residence ranges are also expected to differ between migratory systems, with losses of approximately 65%, 72%, and 86% for Nearctic-Neotropical, Neotropical austral, and Intra-tropical migrants, respectively (Fig. 2, climate model in mixed model selection, supplementary material Table S3). The proportion of partial migrants, i.e., migrant species that also have permanent residence ranges, was higher for Intra-tropical ($n = 10$, 91%) and Neotropical austral ($n = 29$, 72%) migratory systems than for the Nearctic-Neotropical migratory system ($n = 15$, 51%). Many species would remain only in their range of permanent residence ($n = 16$, 31%), losing their breeding and/or

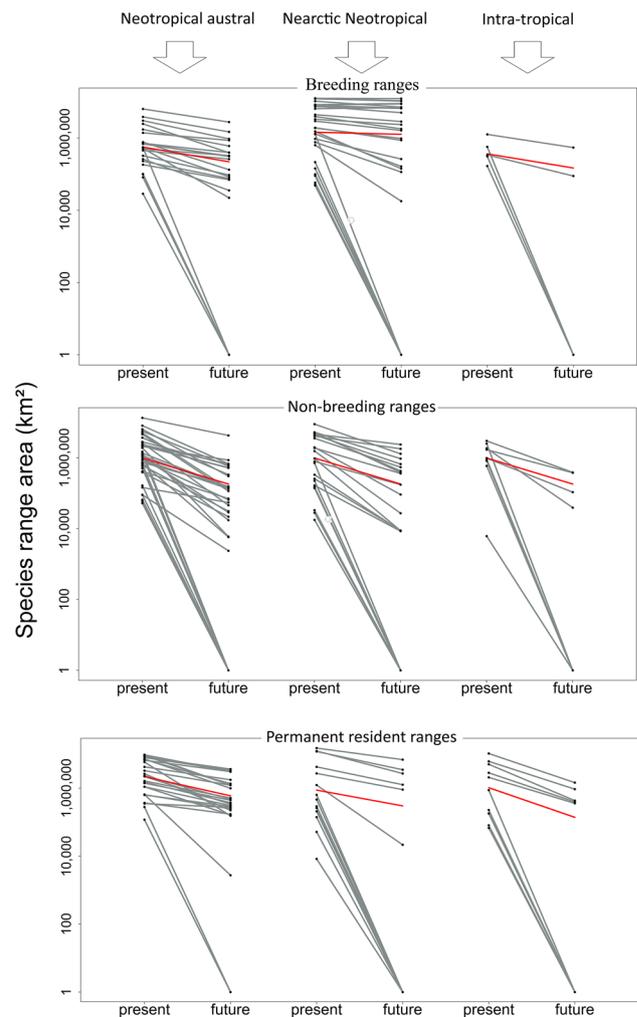


Fig. 2 Predicted changes in the size of breeding, non-breeding, and permanent residence areas of flycatchers (Tyrannidae) by migratory system (Neotropical austral, Nearctic-Neotropical and Intra-tropical migratory systems), under the high emissions scenario (RCP 8.5). Black points represent the area occupied by each species. Gray lines represent the change in size of area between present and future (RCP 8.5) and red lines represents the mean, both estimated by the best fit mixed model (Δ AIC) for each case. For non-breeding areas, there are differences only between the present and future, and for breeding and permanent residence areas there are differences between migratory systems and between the present and future (y-axis scale is in log base 10)

non-breeding ranges (Table 1). Observed median range size for the present and the future estimates are available in supplementary material Table S4.

Shifts in range location

Future predicted occurrence ranges exhibited significant shifts about the centroid positions relative to the present (Fig. 3). The only change in displacement distance that differed between migratory systems was in breeding range,

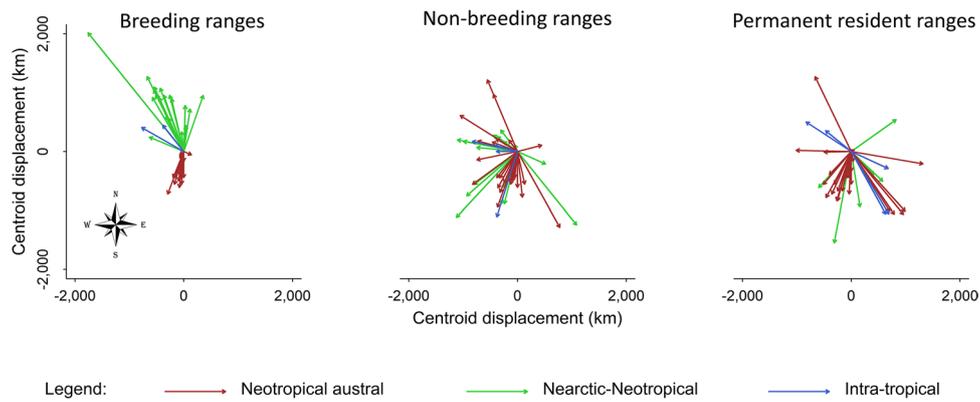


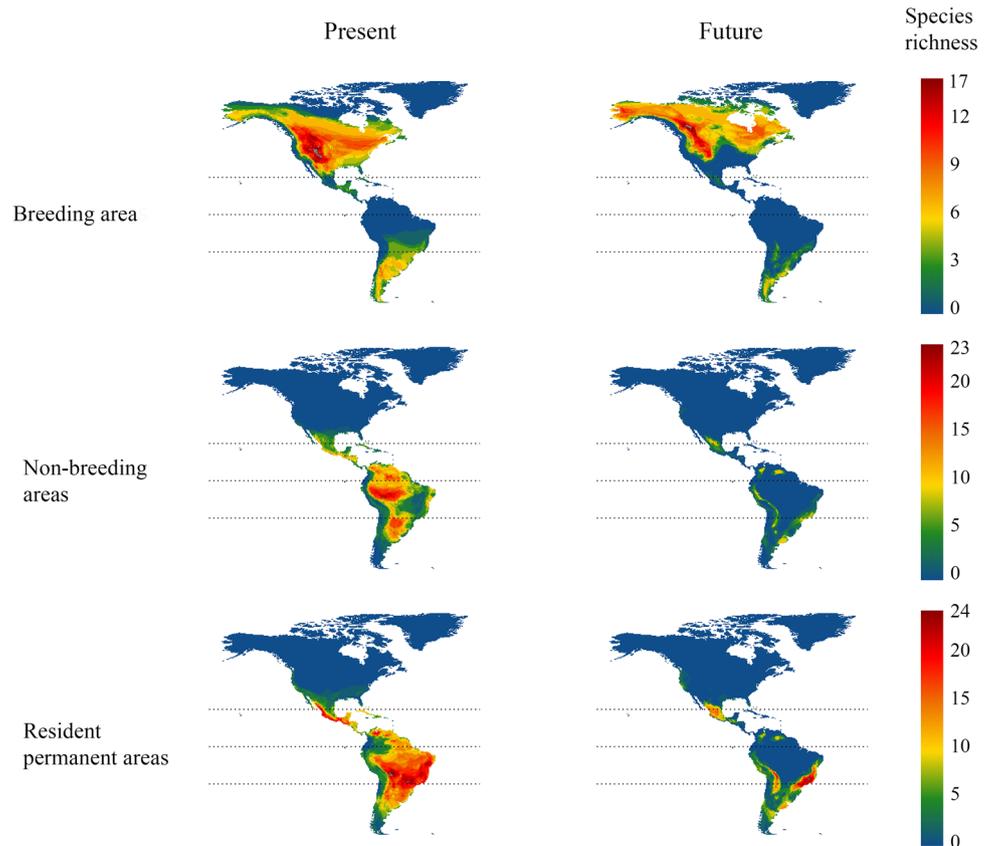
Fig. 3 Shifts in centroid displacement direction and distance of breeding, non-breeding, and permanent residence areas for New World migratory flycatchers (Tyrannidae). The direction of arrows indicates the changes in centroid position from the present (the zero

point in the *x*- and *y*-axis) to the future prediction under the high emissions scenario (RCP 8.5). The size of the arrows indicates the predicted distance for the displacement of the centroid (*x*- and *y*-axis)

driven primarily by breeding range displacement of Neotropical austral migrant species, which are predicted to move approximately 390 km southwards (± 175 km—95% CI) (Fig. 3a and 4, supplementary material Table S5 and S6). For this migratory system, the regions that are expected to maintain the largest number of breeding ranges will be Argentina’s Pampa and Patagonia regions (Fig. 4). In contrast, the breeding ranges of Nearctic-Neotropical migrant

species are predicted to move 1020 km to the north (± 161 km—95% CI), greatly decreasing the number of breeding ranges in the South and Midwest of the USA, and maintaining stable in the Rocky Mountains region (Fig. 4, supplementary material Table S6). Those of Intra-tropical migrant species are predicted to move an average of 734 km in no definite direction (Fig. 3, supplementary material Table S6).

Fig. 4 Species richness map of migratory New World flycatchers (Tyrannidae) showing present and predicted future areas under the high emissions scenario (RCP8.5) of breeding, non-breeding, and permanent residence ranges. All migratory systems are shown together (Neotropical austral, Nearctic-Neotropical and Intra-tropical)



The displacement distances of non-breeding and permanent residence ranges are similar across all migratory systems (supplementary material Table S5), with a mean displacement of approximately 730 km and 850 km, respectively (Fig. 3). Non-breeding ranges show a clear displacement direction to the west in the Nearctic-Neotropical migrant system and to the southwest in the Neotropical austral migrant system (supplementary material Table S6). In general, non-breeding ranges are expected to decline sharply throughout the Amazonian and Gran Chaco regions. The non-breeding ranges remaining climatically suitable are predicted to move towards highland regions (such as the Andes in Colombia, Peru and Bolivia, the Guiana Shield, the Sierra Madre Occidental in Mexico, and the highlands of southeastern Brazil) or towards the south in the Pampas grasslands of Argentina (Fig. 4).

Permanent residence ranges should also decrease in Amazonia and in the Brazilian Cerrado, remaining suitable mostly closer to the Andes of Bolivia and northern Argentina, and in southeastern Brazil. Some regions of Mexico are also expected to remain climatically appropriate as permanent residence ranges (Fig. 4).

All three ranges occupied by Neotropical austral migrants are predicted to move in a southern/southeastern direction (Fig. 3, supplementary material Table S6), with the non-breeding and permanent residence ranges experiencing a larger displacement (730 and 850 km, respectively) relative to the breeding ranges (supplementary material Table S5 for linear model selection and Table S6 for displacement direction averages and Rayleigh test results). Observed median displacement distances between present and future estimates are available in the supplementary material Table S7.

Shifts in migration distance

Current average migration distances between breeding and non-breeding ranges are significantly longer for Nearctic-Neotropical migrants (4143 ± 414 km, mean \pm SE) than for Neotropical austral migrants (1972 ± 443 km, mean \pm SE; $z = -3.581$, $p = 0.001$; Fig. 5), and these migratory distances are predicted to change differently for each migratory system (interaction Δ AIC for mixed model selection, supplementary material Table S8). Results show increases of 1195 ± 426 km (mean \pm SE) for the Nearctic-Neotropical migratory

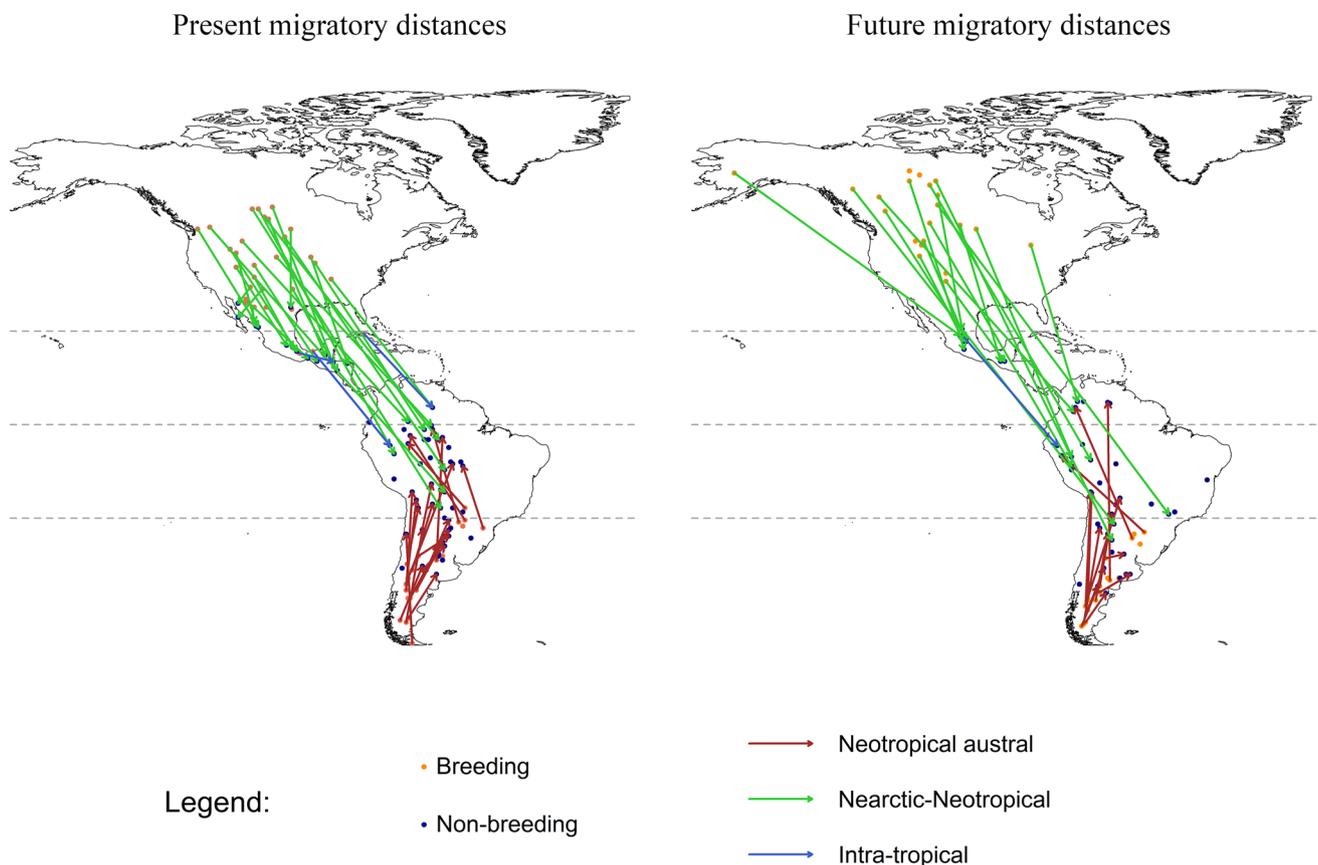


Fig. 5 Migration distances of New World flycatchers (Tyrannidae) across migratory systems in the present and the future in high emissions scenarios (RCP8.5). Each point represents the centroid of

breeding and non-breeding ranges, with arrows indicating the migration distance between ranges

system (about 28%, pairwise comparison for this migratory system $z = -6.807$, $p < 0.0001$; Fig. 5), whereas the increase in distance in other systems was not significant ($p = 0.24$ for Neotropical austral and $p = 0.36$ for Intra-tropical migratory systems). Many species in the future projection completely lost one of their ranges; in these cases, it was not possible to analyze the difference in migration distance between the present and the future.

We restricted migration distance analysis between breeding and non-breeding ranges, excluding distances between these and permanent residence ranges. These are the most biologically relevant migratory routes, and there are very few species predicted to maintain ranges of permanent residence as well as either breeding or non-breeding ranges in the future. Observed median migratory distance for the present and the future estimates from high and low emission climate models are available in the supplementary material Table S9.

Discussion

After modeling the current and future distributions of 80 species in the largest family of birds on the planet, the New World flycatchers (Tyrannidae), results show a clear difference in the way climate change might impact their migratory systems, as a combined effect of climate change and geography of continents. In general, climatically appropriate ranges are projected to be smaller in the future. Additionally, differences found between Neotropical austral and Nearctic-Neotropical migratory systems show an interaction between climate change and the shapes of the North and South American landmasses, as we predicted. Due to the predicted northward displacement of breeding areas in the large landmass of North America, migratory distance increases for Nearctic-Neotropical species. Meanwhile, we predict large decreases in the breeding areas of Neotropical austral migrant species, which would be pushed southwards (see below).

Potential-predicted reductions in the breeding ranges of Neotropical austral migrant flycatchers are strongly related to the displacement of these ranges (by about 400 km, from latitude 36°S to 40°S). The ranges of birds in southern South America are relatively small as a result of the southwards narrowing of South America (Hawkins and Diniz-Filho 2006), a pattern that we predict will be exacerbated by climate change, since they will need to shift southwards. Similar to tropical bird species having to move uphill due to recent climate change (Freeman et al. 2018), we predict a similar process of loss of breeding area for species breeding in the southern cone of South America. The reductions in the size of these southern breeding ranges (on average 60%) are of particular concern, since they represent proportionally

greater losses than the breeding ranges of Nearctic-Neotropical migrant species (12%), whose breeding ranges are on average nearly 2.5 times larger. This shrinking in area is also concerning because it may increase intra- and interspecific competition in the remaining areas (Ahola et al. 2007). Similar effects of climate change have been observed in boreal breeding ranges (Wauchope et al. 64), in addition to changes in timing and duration of the breeding season (Halupka and Halupka 2017).

On the other hand, results indicate that reductions in non-breeding ranges might lead to changes in community richness and composition within the Amazon Basin, with regions in the vicinity of the Andes having the richest non-breeding bird communities. Areas where the non-breeding ranges should move to, or where they should remain, coincide with regions where precipitation is expected to remain steady or increase in the austral winter (Christensen et al. 2013). Although displacement of species to higher altitudes is a general trend (Parmesan 2006), the remaining areas for many species in our study will be largely restricted compared to current distributions (Fig. 4). The sharp altitudinal climatic gradient in the Andes would generate a narrow, suitable area that may need to be protected for the survival of future populations. As indicated by Schaefer's survival and behavioral models (Schaefer 2019) changes such as diminished levels of food resources at non-breeding sites may lead to delays in the timing of breeding and low rates of accumulation of energetic deposits increasing mortality of migratory birds. In addition changes in phenology and abundance of resources caused by climate change can lead to phenological mismatches during the non-breeding season which is of great concern for the conservation of long-distance migrant species (Albert et al. 2020).

Migratory distances may also change as a consequence of the displacements of the breeding and non-breeding ranges. Results show that Nearctic-Neotropical migrant species will increase their migratory distance (1020 km on average), which is consistent with projections for other long-distance migratory species breeding in the northern hemisphere (Zurell et al. 66). Movement of species to higher altitudes and latitudes has been shown to be a global trend caused by temperature increases (Tellería et al. 59; Rushing et al. 2020). Specifically, northern North America, where we forecast the displacement of breeding areas, should see an increase in precipitation by the end of the current century (Christensen et al. 2013). This translates to changes in mean breeding latitudes and a displacement of the southern breeding range margin northward (but not of the northern breeding range margin). This trend has been observed since the mid-1980s for Nearctic-Neotropical migrants in North America (Rushing et al. 2020), supporting our findings and indicating that such changes are already underway. These changes are complex and are evident in the population

trends of North and Central American bird families across biomes. Among migratory bird species breeding in North America, about 2.5 billion individuals have been lost since the 1970s, due to many threats (Rosenberg et al. 2019). Although spring migrants in North America appear to be advancing their timing of spring migration and reproduction in response to climate change (Usui et al. 60; Horton et al. 2019), future longer distance migrations we predict for flycatchers could hamper their ability to properly time their arrival on the breeding grounds.

Conversely, results also showed reductions in migration distance (365 km on average) between the breeding and non-breeding ranges for six Neotropical austral migrant species. This is another scenario in which birds might reduce migratory activity, as has occurred during the evolutionary history of Passeriformes (Dufour et al. 2020). Finally, results show that Intra-tropical migrant species would lose a large percentage of their ranges (Table 1). Normally, Intra-tropical migratory birds are not included in studies of the future impacts of climate change (but see Şekercioğlu et al. 2012), so results of the present study are novel and show that these species would also need to adapt to new conditions. For these species, precipitation changes would impact their populations (Brawn et al. 2017). Thus, further research is needed to better understand the future conservation needs of tropical ecosystems.

We found substantial system-level variation of the impacts of future climate change within the largest family of birds in the New World. The survival of a migratory species in a given habitat depends on such factors as availability of resources, segregation of sex and age within populations, predation level, degree of site fidelity and correctly timing arrival and departure on migration. We have only focused here on the effects of large-scale climatic drivers on the distribution and migration patterns of flycatchers, with resulting impacts possibly being compounded by changes in other niche components and associated variables. Climate models point to substantial changes on our planet during the next decades and organisms are likely to face challenges involving interactions between climate change and in how humans use land, including over-exploitation, habitat loss, pollution, and biological invasions (Oliver and Morecroft 2014).

In summary, we show that impacts of climate change on migratory flycatchers are not homogeneously distributed across space. We suggest that Neotropical austral migrant flycatchers will lose most of their breeding range area, Nearctic-Neotropical migrant flycatchers will need to fly longer distances, and Intra-tropical migrant flycatcher species will face extreme climatic change within their current ranges, requiring them to make substantial range shifts. In any case, current and future threats facing different migratory populations involve a complex set of temporally, spatially, and taxon-dependent relationships (Faaborg et al.

2010). We particularly advocate for monitoring tropical birds and measuring their potential adaptations and behavioral responses to ongoing climatic change, as they are a neglected set of species in climate change studies.

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Author contribution M. R. B., S. V., R. L., and A. E. J. conceived the study; M. R. B., S. V., and L. R. J. developed the modeling, and M. R. B. and L. R. J. analyzed the results. M. R. B. wrote the manuscript. All authors reviewed the manuscript.

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Availability of data and material The data are available at <https://github.com/IsaBraga/bird-migration-and-climate-change>.

Code availability All data processing, models and analysis were done in the R environment (R Core Team 2019). The scripts are available at <https://github.com/IsaBraga/bird-migration-and-climate-change>.

Declarations

Competing interests The authors declare no competing interests.

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