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RESEARCH ARTICLE

Future climate change will impact the size and location of breeding and wintering areas of migratory thrushes in South America

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ABSTRACT

Bird migration patterns are changing worldwide due to current global climate changes. Addressing the effects of such changes on the migration of birds in South America is particularly challenging because the details about how birds migrate within the Neotropics are generally not well understood. Here, we aim to infer the potential effects of future climate change on breeding and wintering areas of birds that migrate within South America by estimating the size and elevations of their future breeding and wintering areas. We used occurrence data from species distribution databases (VertNet and GBIF), published studies, and eBird for 3 thrush species (Turdidae; *Turdus nigriceps*, *T. subalaris*, and *T. flavipes*) that breed and winter in different regions of South America and built ecological niche models using ensemble forecasting approaches to infer current and future potential distributions throughout the breeding and wintering periods of each species. Our findings point to future shifts in wintering and breeding areas, mainly through elevational and longitudinal changes. Future breeding areas for *T. nigriceps*, which migrates along the Andes Mountains, will be displaced to the west, while breeding displacements to the east are expected for the other 2 species. An overall loss in the size of future wintering areas was also supported for 2 of the species, especially for *T. subalaris*, but an increase is anticipated for *T. flavipes*. Our results suggest that future climate change in South America will require that species shift their breeding and wintering areas to higher elevations in addition to changes in their latitudes and longitude. Our findings are the first to show how future climate change may affect migratory birds in South America throughout the year and suggest that even closely related migratory birds in South America will be affected in different ways, depending on the regions where they breed and overwinter.

Keywords: climate change, ecological niche models, migration, Turdidae, South America

LAY SUMMARY

- Bird ranges are changing worldwide due to current global climate changes.
- Bird migration is common in South America, with more than 200 species of Neotropical austral migrants, yet we still understand little about how these species are impacted by climate change.
- We modeled future breeding and winter distributions of 3 species of migratory thrushes in South America.
- Our results suggest that future wintering and breeding areas for migratory birds in South America will decrease, change in latitude and longitude, and shift to higher regions although patterns will likely vary by species.

No futuro as mudanças climáticas afetarão o tamanho e a localização das áreas de reprodução e invernada de sabiás migratórios na América do Sul

RESUMO

Os padrões de migração das aves estão mudando em todo o mundo devido às mudanças climáticas globais atuais. Abordar os efeitos de tais mudanças na migração de aves na América do Sul é particularmente desafiador, uma vez que os detalhes sobre como essas aves migram dentro dos Neotrópicos geralmente não são bem compreendidos. Aqui, pretendíamos inferir os efeitos potenciais das mudanças climáticas nas áreas de reprodução e invernada de aves migratórias da América do Sul, estimando o tamanho e o local de suas áreas de reprodução e invernada no futuro.

Utilizamos dados de ocorrência de bancos de dados online (VertNet e GBIF, eBird), além de estudos publicados em periódicos, de três espécies de sabiás da América do Sul (Turdidae; *Turdus nigriceps, T. subalaris e T. flavipes*) e construímos modelos de nicho ecológico para inferir as distribuições potenciais atuais e futuras ao longo dos períodos de reprodução e invernada de cada espécie. Nossos resultados apontam para mudanças futuras nas áreas de invernada e reprodução dessas espécies, principalmente por meio de mudanças altitudinais e longitudinais de suas áreas de distribuição. A área de reprodução da espécie *T. nigriceps*, a qual migra ao redor da Cordilheira dos Andes, será deslocada para o oeste no futuro, enquanto os deslocamentos de áreas reprodutivas para o leste são esperados para as outras duas espécies. Uma perda geral do tamanho das áreas de invernada no futuro também foi prevista para duas das espécies estudadas, especialmente para *T. subalaris*, e também foi observado um aumento de área para a espécie *T. flavipes*. Nossos resultados sugerem que as mudanças climáticas futuras na América do Sul exigirão que essas espécies mudem suas áreas de reprodução e invernada para altitudes mais elevadas, além de mudanças latitudinais e longitudinais. Nossas descobertas são as primeiras a mostrar como mudanças climáticas podem afetar as aves migratórias na América do Sul no futuro, e sugerem que mesmo aves aparentadas serão afetadas de maneiras diferentes dependendo da região onde se reproduzem e passam o inverno na América do Sul.

Palavras-chave: mudanças climáticas, migração, América do Sul, aves, Modelos de Nicho Ecológico

INTRODUCTION

Recent years have witnessed an increase in the number of studies on the negative impact of current and future rapidly changing environmental conditions on biodiversity (Bellard et al. 2012, Scheffers et al. 2016, Trisos et al. 2020). Such changes may not only affect species richness and their abundances, but also morphological and physiological traits, ecosystem functions, community assembly, and species distributions (Pecl et al. 2017). Global climate change can also impact movement behavior—especially latitudinal and altitudinal movements—as a result of changes in the location and size of areas suitable for breeding, wintering, and migrating (Thomas et al. 2004, Bellard et al. 2012, Vergés et al. 2014).

Across vertebrate species, movement behavior is tightly linked to climatic seasonality (Parmesan and Yohe 2003, Parmesan 2006, Scheffers et al. 2016). Although migratory species have adapted to track seasonal resource availability, they can be particularly vulnerable to rapid environmental change because they move between geographical areas that are influenced by a complex set of environmental factors that vary across time and space and are often hard to predict (Newton 2008). Long-distance migrants are thought to be particularly vulnerable to rapid climate change because they have shown less flexibility in migration timing in the face of climate change, as compared to short-distance migrants (Both et al. 2010, Jones and Cresswell 2010, Végvári et al. 2010; but see Jonzén et al. 2006, reviewed by Knudsen et al. 2011). Nevertheless, numerous migratory birds have already been found to be responding to rapid global climatic changes (Pulido and Berthold 2010, Sekercioglu et al. 2012, Zurell et al. 2018), for example by shifting the location of their wintering and breeding areas (Coppack et al. 2003, Huntley et al. 2006, Zurell et al. 2018, La Sorte et al. 2019) and switching from migration to year-round residency (Fiedler et al. 2004, Niven et al. 2004, Pulido and Berthold 2010).

Bird migration is common in South America, with more than 200 species of Neotropical austral migrants that breed at south-temperate latitudes and that overwinter closer to the Equator (Chesser 1994, Jahn et al. 2013). Two other migratory systems found in South America are altitudinal and intra-tropical migration. Intra-tropical migrants only migrate within the tropics (i.e. between the tropics of Cancer and Capricorn), with movements that are complex and varied (altitudinal, latitudinal, and longitudinal movements). Altitudinal bird migration is common in the Neotropics, consisting of birds breeding at higher elevations and overwintering at lower elevations (Faaborg et al. 2010, Barçante et al. 2017). As is true of avian migratory systems on other continents, the main driver of bird migration in South America is the need to track large-scale spatiotemporal variation in resource availability (Chesser 1994, Joseph 1997, Faaborg et al. 2010, MacPherson et al. 2018). Indeed, despite the wide variety of avian migratory systems found in the Southern Hemisphere, most are still poorly understood, in large part due to their complexity, which are in turn related to demographic- and population-specific migratory strategies (reviewed by Jahn et al. 2009).

One of the main biogeographical differences between Neotropical austral migrants and Nearctic–Neotropical migratory birds that breed in North America is in the relative size of their breeding and wintering areas. The breeding area of most Nearctic–Neotropical migrants (i.e. North America) is overall larger than their available wintering area (i.e. Middle America, northern South America), whereas the opposite is true for most Neotropical austral migrants, because South America is much narrower at south-temperate vs. tropical latitudes (Chesser 1994). Additionally, due to the stabilizing effect of the oceans that make up the majority of the Southern Hemisphere (Yom-Tov et al. 1994, Dingle 2008), the climate at south-temperate latitudes is more seasonally buffered than that at north-temperate latitudes (Paruelo et al. 1998). As a result, Neotropical austral migration generally occurs over shorter distances than does Nearctic–Neotropical migration (Stotz et al. 1996, Jahn et al. 2004, Sekercioglu et al. 2008, Faaborg et al. 2010). Given the different climatic and geographic contexts that migratory birds in South America live within as compared to their north-temperate counterparts, an evaluation of the potential for climate change to affect such populations throughout their annual cycle offers a broader perspective on the potential effects of climate change on birds across the planet and throughout the year (La Sorte and Jetz 2010, Marra et al. 2015).

We aimed to evaluate how the distribution of breeding and wintering areas of migratory birds in South America may be affected under future climate change. *Turdus* thrushes are an ideal model, because they are common migrants on the continent; are found in a wide variety of habitats, including urban areas (Pizo 2007, Gasperin and Pizo 2009); and are relatively easy to identify, such that reliable occurrence data from various sources are available. *Turdus* thrushes also migrate in 3 major migratory flyways on the continent: short-distance Atlantic Rainforest altitudinal migration, in which birds migrate altitudinally within the Atlantic Rainforest (e.g., *Turdus flavipes*; Maia-Gouvêa et al. 2005, Alves 2007); long-distance Atlantic Rainforest migration, a type of intra-tropical migration in which birds migrate latitudinally within the Atlantic Rainforest (e.g., *Turdus subalaris* in Brazil; Vogel 2014); and long-distance Andean migration, a type of Neotropical austral migration in which birds migrate latitudinally along the Andes Mountains (e.g., *Turdus nigriceps* in Argentina; Capllonch et al. 2008).

We hypothesized that future climate change will affect the distribution of the breeding and wintering areas (Figure 1) of long- vs. short-distance migrant *Turdus* thrushes in different ways. Specifically, we expected that the long-distance Andean migrant (*T. nigriceps*), which migrates along the Andes mountains (hereafter, the Andean migratory flyway) would experience displacements of breeding and wintering areas to higher elevations, since higher elevations in the Andes Mountains are in the vicinity of its current range (Figure 1A). We expected that the long-distance Atlantic Rainforest migrant (*T. subalaris*), which migrates latitudinally within the Atlantic Rainforest (hereafter, the Atlantic Rainforest migratory flyway), would experience a reduction of breeding and wintering areas (Figure 1B), since predicted changes in annual rainfall levels in this region, including a prolonged dry season (Scarano and Ceotto 2015), should result in decreases in the breeding and wintering areas of tropical birds (Shaw and Kelly 2013, Xu et al. 2017). We also expected that the short-distance altitudinal migrant (*T. flavipes*), which migrates altitudinally within the Atlantic Rainforest (hereafter, the short-distance altitudinal migratory flyway), would experience a less pronounced reduction in breeding and wintering areas than the 2 long-distance migrants because local-scale processes, such as habitat fragmentation and loss, which is widespread in the Atlantic Rainforest biome (Ribeiro et al. 2009), tend to have a greater influence on short-distance migratory strategies than processes that operate at larger spatial scales, such as climate change (Dirnböck et al. 2003; Figure 1C). We conclude with suggestions for future directions for climate vulnerability assessments for migratory birds in South America, where the vulnerability of migratory birds to current and future climate change throughout their annual cycle is still poorly known.

METHODS

We applied ecological niche modeling (ENM) approaches to predict the current potential distribution of breeding and wintering areas and simulate the effects of future climate change on the breeding and wintering areas of 3 migratory thrush species (i.e. *T. nigriceps*, *T. subalaris*, and *T. flavipes*). We gathered current and future bioclimatic data from WorldClim 1.4 (Hijmans et al. 2005) to assess current and future climate scenarios. We then integrated occurrence data and bioclimatic data with 4 mathematical algorithms and conducted an ensemble forecasting approach to predict future shifts in breeding and wintering ranges in these species (Peterson et al. 2011). Although these ENMs do not account for the effects of land cover or non-climatic factors (i.e. dispersal or biotic interactions), the effects of climate are a reliable projection of effects of climate change at these spatial scales.

Species Occurrence Data

Species occurrence data were obtained from eBird, which uses automated filters and regional editors to ensure data quality (Sullivan et al. 2014). The species we studied are highly vocal in summer and often occur in open habitats in winter, increasing their chance of detection. Nevertheless, errors of omission by observers in eBird (due to observers not being present when the study species is present or when the observer and study species are both present, but the latter goes undetected; Johnston et al. 2019) pose a potential bias in our analysis. We evaluated potential bias in eBird observer coverage by using the Global Human Footprint Index (HFI; Venter et al. 2016) and detected a tendency for a higher HFI during winter for *T. flavipes* and *T. subalaris*, with the opposite pattern in *T. nigriceps* (Supplementary Material Information S1). This suggests that coverage by observers in eBird may be lower during the breeding season for *T. flavipes* and *T. subalaris* and lower during winter for *T. nigriceps*. We therefore accessed

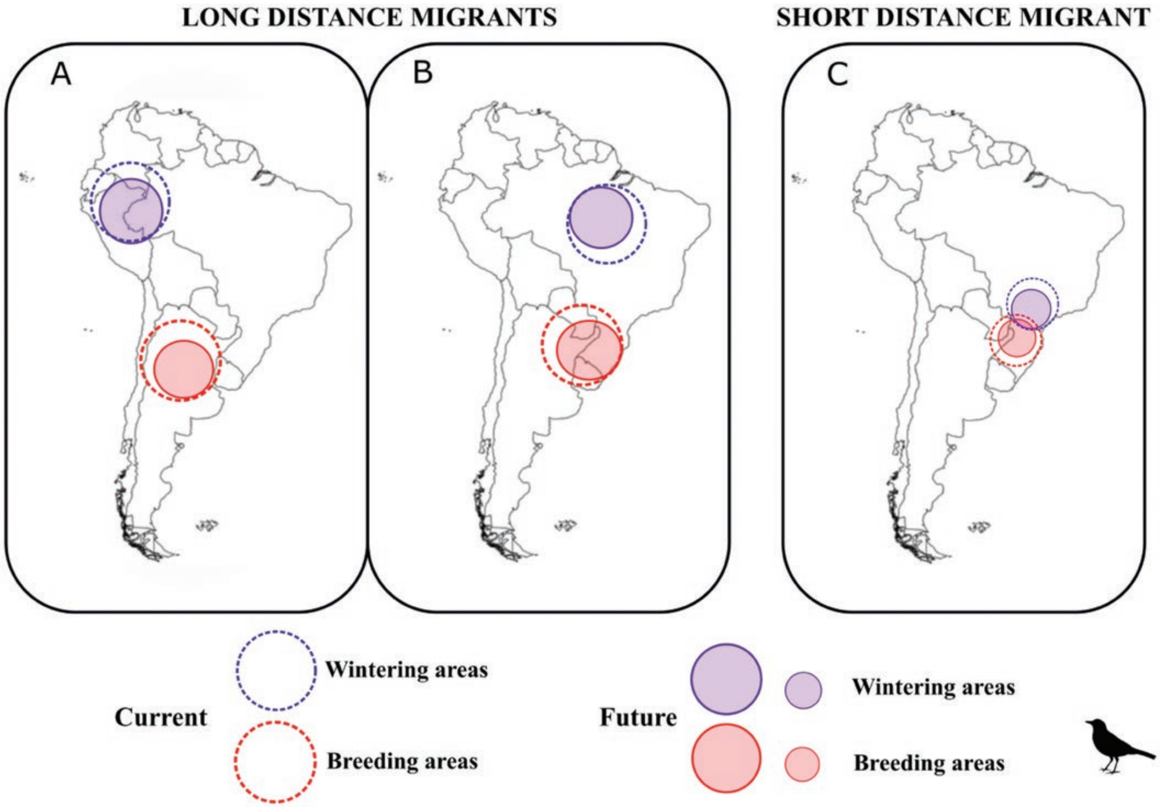

FIGURE 1. Predicted effects of future climatic changes on the size and location of wintering and breeding areas of migratory *Turdus* thrushes in South America: (A) a long-distance Andean migrant (*T. nigriceps*), (B) a long-distance Atlantic Rainforest migrant (*T. subalaris*), and (C) a short-distance altitudinal migrant (*T. flavipes*).

online databases, the Global Biodiversity Information Facility (GBIF) and VertNet, because the use of such databases has been shown to improve data coverage (Spears 2017). Finally, we supplemented species occurrence data using published studies (Mestre et al. 2011, Somenzari et al. 2011).

Available occurrence data range from 1980 to 2017 and were divided into 2 categories: breeding areas (spring and summer; September to March) and wintering areas (May to August) (Supplementary Material Figure S1). This division was based on the date and location (longitude and latitude) of sampling events of individual birds and on information available in the literature on the annual cycles of these species (*T. nigriceps*, Capllonch et al. 2008; *T. subalaris*, Mestre et al. 2011, Somenzari et al. 2011, Vogel 2014; *T. flavipes*, Alves 2007; Supplementary Material Table S1). All occurrence records that did not have date and location information were excluded from the analysis, as were duplicate occurrence data and city centroids.

Because occurrence records are often from areas of high human density, we plotted occurrence data in relation to the Global Footprint Index map (Supplementary Material Information S1). We conducted a spatial rarefaction of occurrence data with a minimum distance of 5 km between pixels, to further even out sample bias (clustering) in observer effort. To rarefy the occurrence points, the *Spatially Rarefy Occurrence Data for SDMs* tool from SDMtoolbox 2.4 of Arcgis 10.5 was used (Brown et al. 2017). In total, there were 334 occurrence records (n =334; n = 217 breeding records and n = 117 wintering records).

Climatic Variables

We used 2 different geographic backgrounds to build the ENMs, one for each species, using 2.5 arc-minute cell resolution (~5 × 5 km at the equator), because the ranges of the study species are on the order of hundreds of kilometers square and because elevational gradients in South America occur over tens to hundreds of kilometers. Given differences in the spatial scale of breeding and wintering areas of short- vs. long-distance migrants, we used different background regions to increase ENM accuracy of these migration patterns (see Barve et al. 2011 for more information about background selection criteria).

We used the entire boundaries of South America as a background to build models of long-distance migrations (*T. nigriceps* and *T. subalaris*) and used the Atlantic Rainforest Biome delimitation (Muylaert et al. 2018) to build short-distance migration models. For each delimitation, we downloaded all 19 bioclimates and conducted variable selection using *Factor Analysis* (Sobral-Souza et al. 2015). For the long-distance migration models, we selected 7 bioclimatic variables: Mean Diurnal Range (bio02), Temperature Seasonality (bio04), Max Temperature of the Warmest Month (bio05), Mean Temperature of the Wettest Quarter (bio08), Precipitation of the Driest Month (bio14), Precipitation of the Wettest Quarter (bio16), and Precipitation of the Warmest Quarter (bio18) (Supplementary Material Table S2). For short-distance migratory models (*T. flavipes*) using the Atlantic Rainforest delimitation, we selected 5 variables: Mean Diurnal Range (bio02), Isothermality (bio03), Mean Temperature of the Warmest Quarter (bio10), Precipitation of the Driest Month (bio14), and Precipitation of the Wettest Quarter (bio16) (Supplementary Material Table S3). These climate variables (primarily based on temperature and precipitation) have been shown to impact the ecology and movements of migratory birds in South America (MacPherson et al. 2018) and of tropical birds more generally (Şekercioglu et al. 2012).

To build future predictions and test the future effects of climate changes on breeding and wintering distributions, we used climate projections to 2050 (i.e. the mid-point for the period 2041–2060) and 2070 (the mid-point for the period 2061–2080) for 2 contrasting emissions scenarios (IPCC 2014): (1) IPCC AR-CMIP 5/RCP 4.5 (lower energy demand) and (2) IPCC AR-CMIP 5/RCP 8.5 (i.e. maximum power requirement). We also used 3 different atmosphere–ocean general circulation models (AOGCMs) to generate future climate models: CCSM4, MIROC–ESM, and MRI. We selected these AOGCMs following the protocol of Varela et al. (2015), who suggest the use of different AOGCMs to reduce model uncertainty.

Ecological Niche Models

To predict potential species distributions in current and future climate scenarios, we used ensemble forecasting approaches based on the use of different ENM algorithms (Araújo and New 2007), which reduces the problem of variation inherent with using different types of algorithms that are needed to infer species distributions (Peterson et al. 2011). The ensemble forecast is recommended as a protocol for building ENMs (Araújo et al. 2019) and is a widely used technique (Hao et al. 2019). We used 4 algorithms to infer species distributions: (1) Bioclim (Envelope Score; Nix 1986), (2) Domain (Gower Distance; Carpenter et al. 1993), (3) Maximum Entropy (MaxEnt, 3.3.3k; Philipps and Dudík 2008), and (4) Support Vector Machines (SVM; Tax and Duin 2004). We used these algorithms because we applied 2 presence-only methods (Bioclim and Gower Distance) and 2 machine learning approaches, based on presence and background methods (SVM and MaxEnt; Phillips et al. 2006, Li et al. 2011).

We used True Skill Statistics (TSS) values (Allouche et al. 2006) to conduct model evaluation. The TSS index calculation is based on values of sensitivity and specificity of models, such that it is considered a threshold-dependent index. To calculate TSS values, we inferred the "maximum sensitivity and specificity" threshold, recognized as the best threshold for use of presence-only methods (Liu et al. 2016), as in the case of the present study. To calculate this threshold, we divided the occurrence records into training and test folding, counting 75% and 25% of occurrence records, respectively. This sub-setting procedure was randomized 10 times to decrease the autocorrelation between training and test folding (Peterson et al. 2011) and was run to build current predictions and then to predict future models separately.

We overlapped all maps using the frequency ensemble approach. To do so, we used the maximum sensitivity and specificity threshold value for each model, built to transform the continuous map into a binary map. Thereafter, we concatenated the replicates of the same algorithms, as well as between algorithms. Thus, the number of cells in the final distribution maps shows the standardized frequencies of predicted presences, combining all generated models of each study species for each temporal and emissions scenario, for both breeding and wintering points (Supplementary Material Figure S2).

To evaluate the effects of future climate change on breeding and wintering areas, we transformed frequency maps into binary maps using the least presence threshold (LPT) for wintering and breeding areas, separately. The use of the LPT with the highest sensitivity and very low specificity values (SE = 1) generates areas with no omission error, selecting the area with all the known occurrences of a species in each scenario (Liu et al. 2013). We calculated these LPT values for the current climatic scenario prediction and used those values to generate future scenarios.

All model ensembles were generated in language R (R Development Core Team 2018), using the *bioclim*, *gower*, and *maxent* functions of the *dismo* package (Elith and Franklin 2017), *ksvm* of the *kernlab* package (Karatzoglou et al. 2004), and the *raster* package (Bivand et al. 2019).

Dynamic Changes in Wintering and Breeding Site Distribution Under Climate Change

To evaluate changes in wintering and breeding areas, we constructed histograms of species occurrence as a function of elevation, latitude, and longitude across all temporal scenarios (current, RCP4.5–2050, RCP4.5–2070, RCP8.5–2050, and RCP8.5–2070). We evaluated changes in local suitability by subtracting the values of future models from the present model based on frequency ensemble model pixels to infer areas with increasing and decreasing suitability as a result of future

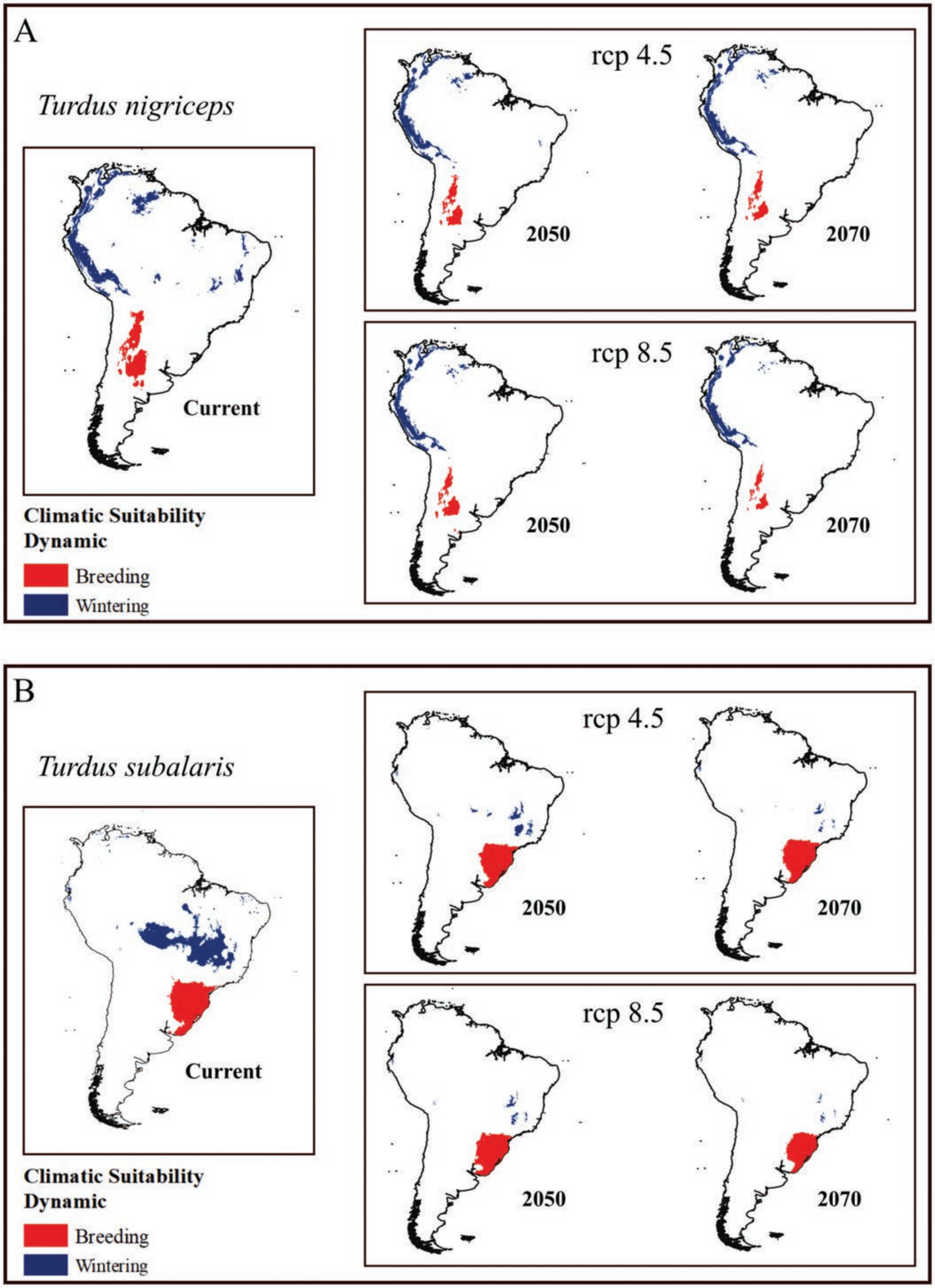

FIGURE 2. Seasonal distributions of 3 migratory *Turdus* thrushes in South America under future climate change scenarios: (A) a long-distance Andean migrant (*T. nigriceps*), (B) a long-distance Atlantic Rainforest migrant (*T. subalaris*), and (C) a short-distance altitudinal migrant (*T. flavipes*). Red bar areas correspond to breeding areas and blue bar areas to wintering areas.

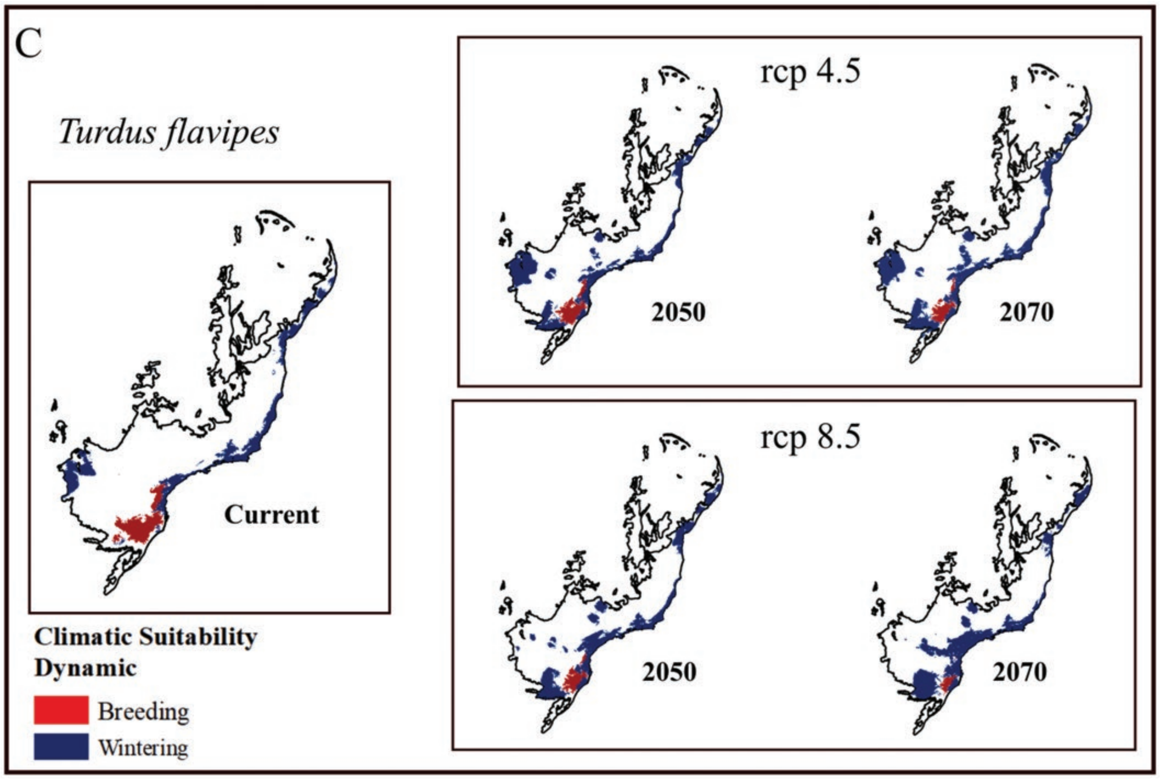

FIGURE 2. Continued.

climate change. To test for changes in elevation, latitude, and longitude of breeding and wintering areas, we built and compared histograms of area values under future vs. current climate scenarios (frequency ensemble models) using a Wilcoxon test, which is a nonparametric statistical test that can be used when the distribution of the differences between the 2 samples cannot be assumed to be normally distributed (Wilcoxon 1946). We separately compared samples from the current vs. future distribution values (for 2050 and 2070) in the 2 emissions scenarios.

RESULTS

Distribution of Wintering and Breeding Areas

All models showed TSS values above 0.5, indicating a good fit. Inferences of the potential current distribution of wintering and breeding areas indicated different patterns for each of the 3 species. *Turdus nigriceps* (Figure 2A) was estimated to breed near the Andes Mountains in Argentina, wintering in the Andes from Peru to Venezuela, and in smaller areas in lowland Brazil (Figure 2A). *Turdus subalaris*, the long-distance Atlantic Rainforest migrant (Figure 1B), was estimated to breed in southern Brazil and to overwinter in small areas in central Brazil (Figure 2B). Small areas of the highest regions of the Southern Atlantic Rainforest appear to be appropriate breeding areas for the short-distance altitudinal migrant (*T. flavipes*; Figure 2C), and a large area of the Atlantic Rainforest was estimated as suitable for it to overwinter (Figure 2C). For future projections, we observed changes in the breeding and wintering areas of the long-distance Andean migrant, losses of suitable winter areas of the long-distance Atlantic Rainforest migrant, and for the breeding areas of the short-distance altitudinal migrant (Figure 2).

Effects of Future Climate Changes on Wintering and Breeding Areas

Our findings suggest that there will be drastic effects of future climate change on the breeding and wintering areas of these 3 South American migratory birds (Table 1; Supplementary Material Figures S3–S8). Overall, our results predict a substantial decrease in wintering area for the long-distance Andean migrant (*T. nigriceps*) and even more so for the long-distance migrant in the Atlantic Rainforest (*T. subalaris*), but not for the short-distance altitudinal migrant (*T. flavipes*), which faces a drastic decrease of its breeding area (Table 1). Additionally, the absolute size of the future area of *T. flavipes* will increase, but in different places relative to its present-day suitable areas, retaining few present-day

TABLE 1. Size of the breeding and wintering areas predicted by present-day and future projection models. The areas are described in absolute size (km^2) and in percentages of area gained or lost. Negative values represent a loss of area as a percentage of the current distribution under future carbon emissions scenarios (RCP 4.5, 2050 and 2060; RCP 8.5, 2050 and 2070) and positive values represent percent area gained.

	Breeding area			Wintering area		
	Turdus nigriceps	*Turdus subalaris*	*Turdus flavipes*	*Turdus nigriceps*	*Turdus subalaris*	*Turdus flavipes*
Current	421,978.16	822,639.02	702,69.31	859,664.22	1,254,138.13	182,116.03
RCP 4.5/2050	249,261.14	784,742.18	51,917.54	559,436.71	211,532.01	311,432.53
RCP 4.5/2070	200,772.30	783,236.93	35,776.75	529,745.23	72,458.32	364,583.03
RCP 8.5/2050	243,986.20	784,580.39	35,968.57	525,486.86	98,528.89	295,207.98
RCP 8.5/2070	132,020.87	614,070.19	14,260.86	478,962.15	40,162.56	335,175.69
Percentage						
RCP 4.5/2050	−41.00%	−4.60%	−26.12%	−34.93%	−83.14%	71.00%
RCP 4.5/2070	−52.50%	−4.80%	−49.09%	−38.38%	−94.23%	100.00%
RCP 8.5/2050	−42.20%	−4.60%	−49.10%	−38.88%	−92.15%	62.09%
RCP 8.5/2070	−68.70%	−25.36%	−79.71%	−44.29%	−96.80%	84.04%

regions in future projections (Supplementary Material Figures S7 and S8).

Our results suggest that future geographical shifts in wintering and breeding areas will occur in relation to elevation, longitude, and latitude (Figures 3–5; Supplementary Material Table S4), with displacements of breeding and wintering areas to higher elevations for all 3 species (Figures 3–5). Indeed, all simulations of future climate scenarios pointed to the displacement of breeding and wintering areas to higher elevations (Figures 3–5). Forecasts showed a longitudinal displacement of the breeding range of the long-distance Andean migrant (*T. nigriceps*) to the west and a marked loss of suitability in its distribution to the east (Figure 3). Notably, although we detected large losses in its overall wintering area, we also noted a gain in suitable areas in the Andes Mountains (Figure 3). Similarly, we noted an overall major decrease in the suitability of the wintering areas of the long-distance Atlantic Rainforest migrant (*T. subalaris*) under future scenarios. Its breeding areas tend to shift to the east and south, accompanied by losses in areas to the west and to the north (Figure 4). Results also indicate a reduction in breeding area for the short-distance altitudinal migrant (*T. flavipes*), but an overall increase in the size of its wintering area. Although it is projected to lose wintering area to the north and west, it should experience gains to the south (Figure 5).

Results of the Wilcoxon tests reinforce patterns observed for the 3 species. In almost all cases, we observed differences between the suitability of the current and future projections ($P < 0.001$), except for latitudinal and longitudinal values in a few cases (Supplementary Material Table S4). Nonsignificant latitudinal changes in breeding areas were observed for the short-distance altitudinal migrant, *T. flavipes*, under both future year's scenarios RCP 4.5 (Current/2050, w = 5222864, P = 0.13) and in the breeding latitude of the long-distance Andean migrant, *T. nigriceps*, under RCP 4.5 (Current/2070, w = 155012843, P = 0.079). For wintering areas, no difference was observed in latitude for the long-distance Atlantic Rainforest migrant, *T. subalaris*, under RCP 8.5 (Current/2050, w = 8128700, P = 0.32). A nonsignificant longitudinal change in breeding areas was observed for the long-distance Andean migrant under both future year's scenarios RCP 8.5 (Current/2050, w = 151125422, P = 0.75). A summary of the results of the effects of future climate conditions on elevation, latitude, and longitude for the 3 species is presented in Supplementary Material Figures S9–S14 and Tables S4 and S5.

DISCUSSION

Our results suggest a drastic effect of future climatic conditions on the wintering and breeding areas of 3 species of thrushes representing 3 migratory bird flyways in South America. Although the projected effects are

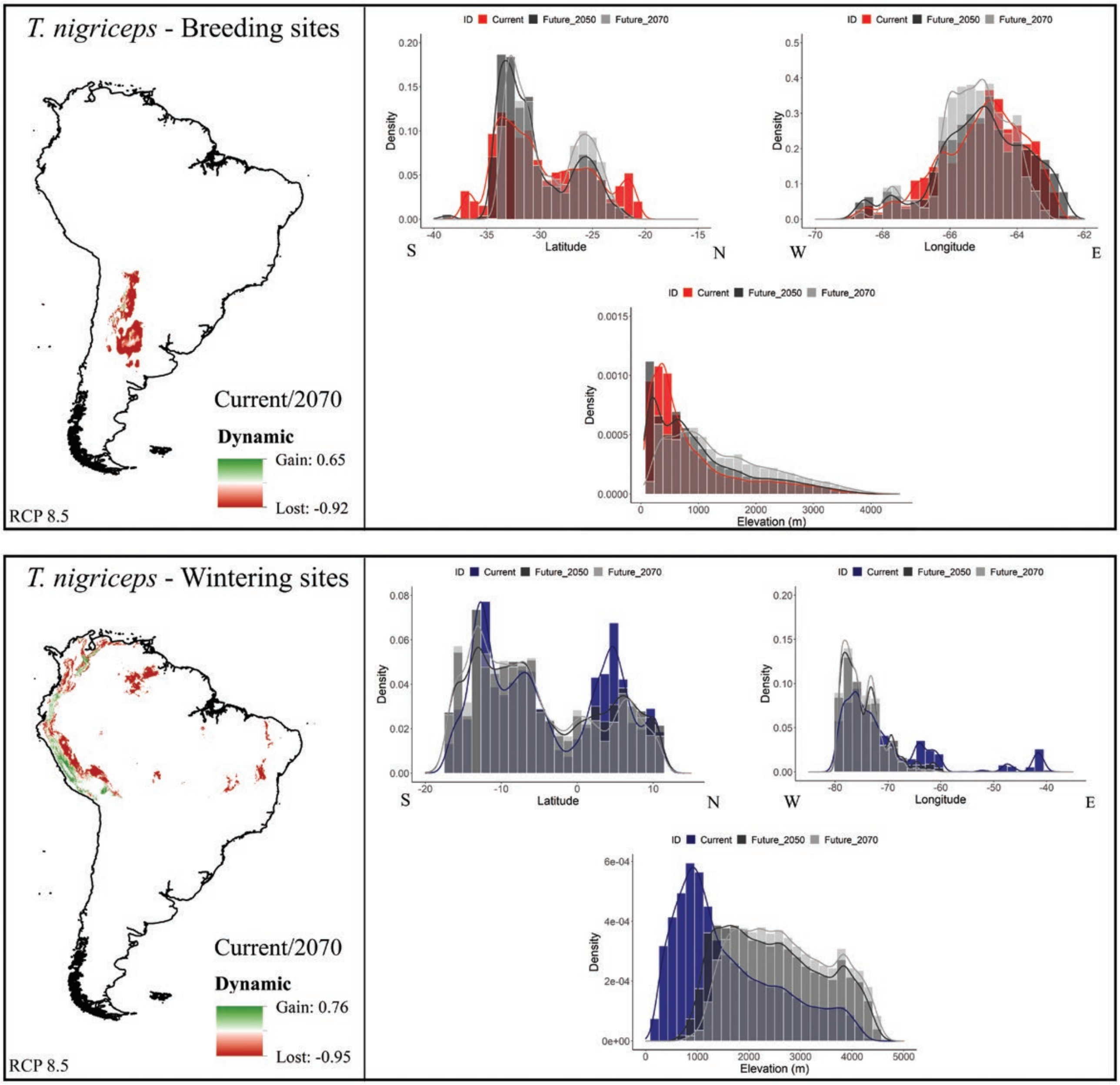

FIGURE 3. Effects of future climate change on wintering and breeding areas across elevation, latitude, and longitude for the long-distance Andean migrant (*Turdus nigriceps)*. Maps on the left show losses or gains in terms of local suitability between current conditions and the most drastic future climate projection (2070, rcp85). Histograms on the right show climate suitability in relation to elevation and longitude/latitude for present-day and future projections under the higher carbon emissions scenario (2050, rcp85; 2070, rcp85). Red bar areas correspond to breeding areas and blue bar areas to wintering areas. Areas in dark gray represent the future scenario for the year 2050 and areas in light gray the future scenario for the year 2070.

different for breeding and wintering areas, our models predict overall reductions in the size of the breeding and wintering areas of migratory birds in South America, with the exception of *T. flavipes*, for which there was an overall gain in wintering area size (Supplementary Material Figure S3). Additionally, our models predict shifts toward higher elevations, as well as shifts in longitude and latitude. Overall, these findings, the first to predict the effects of future climate change on bird migration in South America, point to the negative effects of climate change on seasonal distributions of migratory birds in South America.

Our results point to an overlap of wintering and breeding areas above 800 m, and significant future increases in the wintering area of the short-distance migrant species, *T. flavipes*, which usually overwinters below 800 m

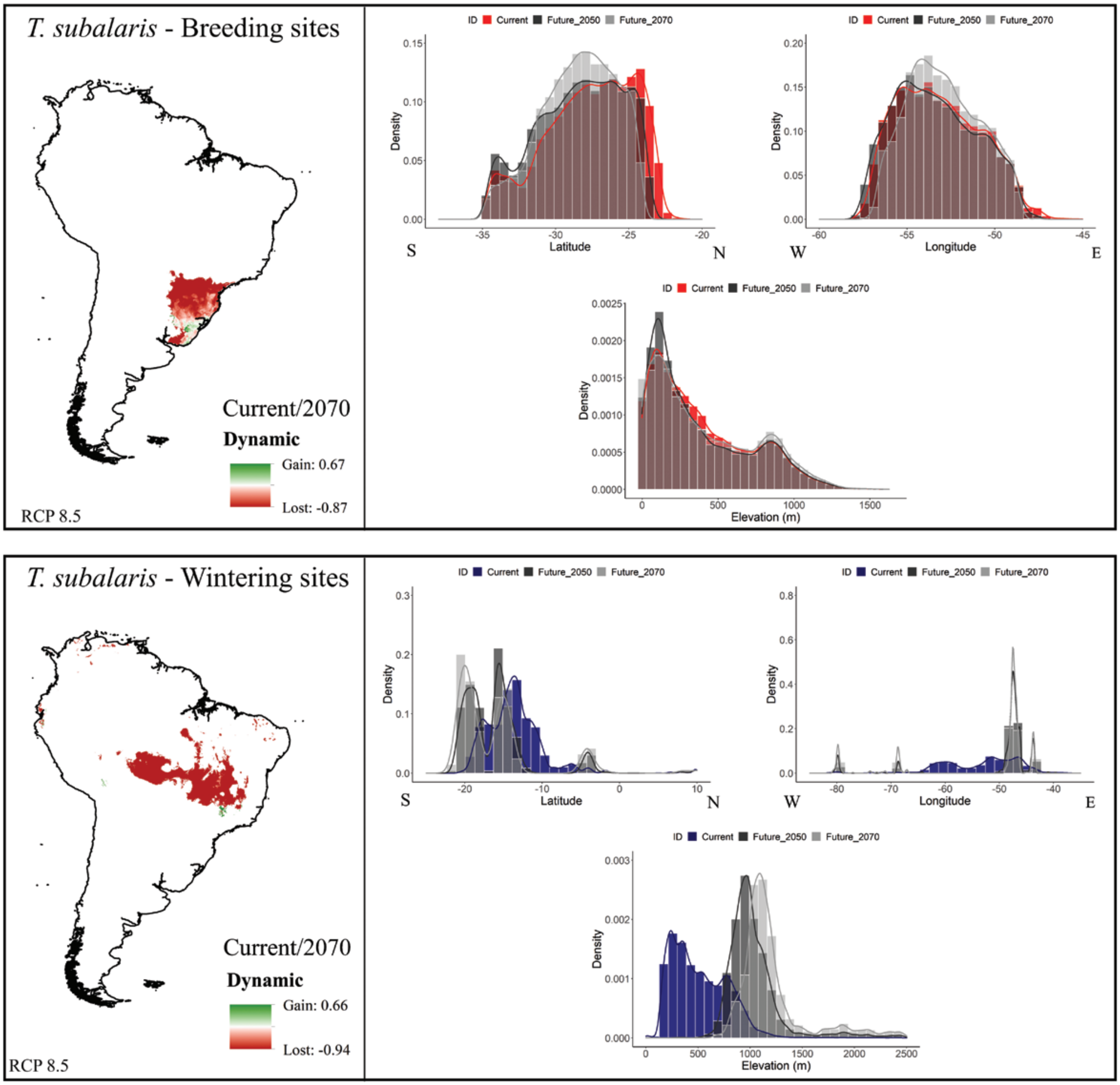

FIGURE 4. Effects of future climate change on wintering and breeding areas across elevation, latitude, and longitude for the long-distance Atlantic Rainforest migrant (*Turdus subalaris*). Maps on the left show losses or gains in terms of local suitability between current conditions and the most drastic future climatic projection (2070, rcp85). Histograms on the right show climate suitability in relation to elevation and longitude/latitude for present-day and future projections under the higher carbon emissions scenario (2050, rcp85; 2070, rcp85). Red bar areas correspond to breeding areas and blue bar areas to wintering areas. Areas in dark gray represent the future scenario for the year 2050 and areas in light gray the future scenario for the year 2070.

elevation (Alves 2007). The best-performing models were observed for the breeding season (Supplementary Material Table S5), mainly due to the quality of breeding season data. As expected, data for wintering areas are scarce in comparison with that for breeding areas, adding to the difficulty of evaluating the spatiotemporal dynamics of wintering areas (Alves 2007).

For the long-distance Andean migrant (*T. nigriceps*), suitable wintering areas were predicted in central Brazil and northern South America, where the species does not occur, which may have occurred in part because this species is closely related to the long-distance Atlantic Rainforest migrant (*T. subalaris*), and both may have similar climatic requirements, increasing the possibility of competitive

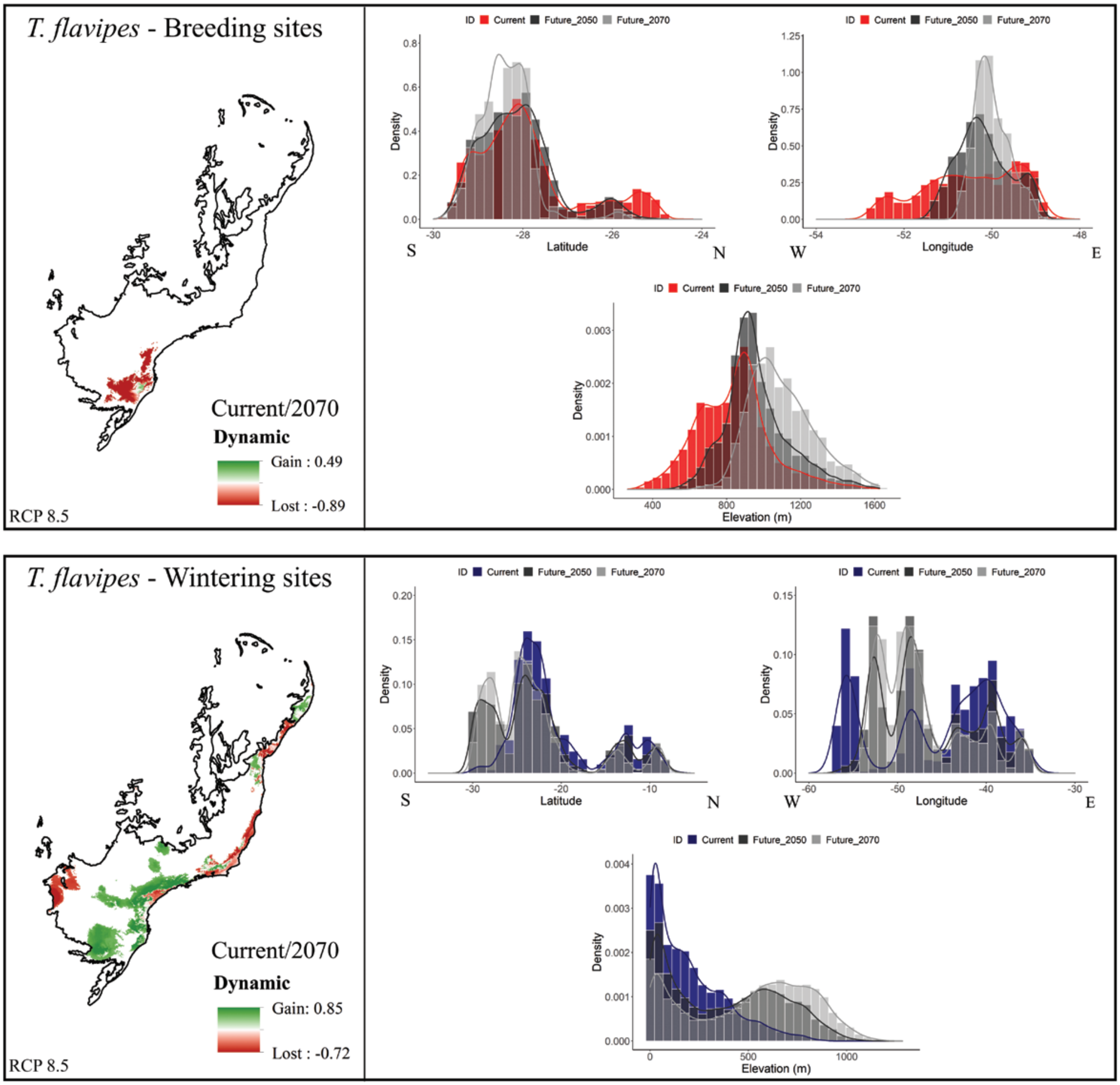

FIGURE 5. Effects of future climate change on wintering and breeding areas across elevation, latitude, and longitude for the short-distance altitudinal migrant (*Turdus flavipes*). Maps on the left show losses or gains in terms of local suitability between current conditions and the most drastic future climatic projection (2070, rcp85). Histograms on the right show climate suitability in relation to elevation and longitude/latitude for present-day and future projections under the higher carbon emissions scenario (2050, rcp85; 2070, rcp85). Red bar areas correspond to breeding areas and blue bar areas to wintering areas. Areas in dark gray represent the future scenario for the year 2050 and areas in light gray the future scenario for the year 2070.

exclusion, as has been found in other Neotropical avian taxa (Gómez-Bahamón et al. 2020).

Effects of Future Climate Changes on Wintering and Breeding Areas

We observed an upslope displacement of suitable areas for both breeding and wintering areas across all future projections. Our findings suggest losses of suitable areas below 1,000 m and gains of suitability in regions higher than 4,000 m in the Andes. The displacement of suitable areas westwards (i.e. higher longitude values) in breeding areas also corroborates the gains in the Andean highlands. Although the availability of area can vary across elevations (Elsen and Tingley 2015), a significant portion of these new suitable areas, especially in the Andean highlands, will not be covered by forest, which would be unsuitable for the 3 forest species we studied (Hansen et al. 2013, Tuanmu and Jetz 2014).

The effects of future climate changes on breeding and wintering areas of long-distance Atlantic Rainforest migrants (Figure 2B) are similar to that predicted for the long-distance Andean migrant (*T. nigriceps*), with a future decrease in the extent of their wintering area. Species that use this flyway are primarily found in winter in lower elevation riparian forest, in the ecotone between the Amazonian and Cerrado biomes (Alves 2007, Vogel 2014). Similarly, their breeding areas will undergo overall size reductions, with projected displacements to the southeast (i.e. toward higher elevations to the east and south; Figure 4). Thus, the longitudinal trend observed in the climatically extreme future projections can be explained by the expansion of breeding areas in southern Brazil, including into higher elevations. Species that are part of the long-distance Atlantic Rainforest flyway tend to inhabit the forest canopy during the breeding season (Clement 2000); however, much of the Atlantic Rainforest is fragmented due to human activities (Ribeiro et al. 2009). Thus, even if our results predict appropriate future climatic conditions for breeding and wintering in the Atlantic Rainforest, their dependency on forest canopy vegetation, combined with high levels of anthropogenic impacts on habitat (Supplementary Material Information S1), including forest fragmentation (Ribeiro et al. 2009), may compromise their future population viability in this region. Additionally, the area available for occupancy can be impacted by local mountain topography (Elsen and Tingley 2015), such that understanding how changes in both available area and habitat can in concert affect future suitability for a given species is a major research challenge.

Dataset and Climate Prediction Models

The use of citizen science databases (e.g., eBird) has provided novel information about migratory bird ecology (Jackson et al. 2015, Lin et al. 2015, Coxen et al. 2017) and has informed ENMs to evaluate the effects of climate on animal communities (Gonçalves et al. 2016, Newbold 2018). Although citizen science data and broad-scale environmental data (e.g., climate scenarios) have limitations (Wiens et al. 2009), the use of citizen science-based occurrence data for South American birds is useful in generating macroecological evaluations when corrections for biases are applied, such as using multiple databases (e.g., VertNet) and by evaluating potential bias using resources such as the Global HFI (Supplementary Material Information S1). The use of such data in bird migration studies is relatively recent (Coxen et al. 2017, MacPherson et al. 2018), such that its full potential has yet to be explored, especially in relatively understudied migratory bird systems, such as Neotropical austral and intra-tropical bird migration.

Our results project future losses of breeding areas of short-distance altitudinal migrants in the Atlantic Rainforest, supporting our prediction of future losses of suitable breeding areas (Figure 1). Species breeding upslope (above 800 m) may need to switch migratory routes if they need to shift their breeding areas to higher elevations (Figure 3). Similarly, other taxonomic groups, such as small mammals (Rowe et al. 2015), other bird species (Freeman and Class Freeman 2014), and amphibians (Bustamante et al. 2005, Raxworthy et al. 2008) are predicted to move to higher elevations. Nevertheless, how these species will adapt to these changes is still an open question. They may be able to adapt by changes in their migratory behavior (Fiedler et al. 2004, Niven et al. 2004, Pulido and Berthold 2010), but the resulting impacts of these changes on their population dynamics are still unknown. In this context, future prediction scenarios may help establish protocols for the conservation of these species over the long term.

In the face of rapid climatic changes, we can expect important changes for a wide variety of species, with some being more impacted than others (Bellard et al. 2012, Scheffers et al. 2016). Large-scale projections may not be equally accurate for all species and less accurate for wintering areas than for breeding areas (Zurell et al. 2018), since winter distributions for many species are not yet fully described. Although the species we studied are not perfectly representative of all types of migratory birds in South America, many bird species on the continent migrate as part of the same migratory systems as the species we studied (Stotz et al. 1996), such that these results indicate novel directions for future research on risks of rapid climate change for a broad suite of migrants. On the other hand, at finer spatiotemporal scales, other non-climatic abiotic factors are likely more important in molding the ecology of species and may even change expected relationships (Spence and Tingley 2020). Considering the potential for high levels of variation in fine-scale landscape scenarios, future studies should focus on gaining a more spatially and temporally detailed understanding of the effects of future climate change on migratory bird species in South America.

The relatively few studies on breeding and wintering areas of avian migrants in the Southern Hemisphere are mainly due to the logistic difficulty associated with tracking organisms at large scales, in addition to the lack of infrastructure for most countries in this region (Jahn et al. 2004). However, emerging technologies and methods, including citizen science-based platforms, are making detailed research on bird migration more feasible across the globe. Additionally, measuring such individual-level variables as flight performance and dispersal ability could go a long way in developing a more robust understanding of how future change is likely to affect different populations across their annual cycle (La Sorte and Jetz 2010). We hope this study will inspire further research on the ecology and conservation of the rich assemblage of migratory birds across the rapidly changing South American landscape.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Ornithological Applications* online.

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Ethics statement: In this research, we used all data from online databases. We follow all protocols established by these databases (Ebird, VertNet, GBIF, and Wordclim 1.4).

Author contributions: N.S.S., T.S.S., M.H.V., A.E.J., and M.A.P. formulated the idea; N.S.S. organized the dataset; N.S.S. and M.H.V. analyzed the data; and N.S.S., T.S.S., M.H.V., A.E.J., and M.A.P. wrote the manuscript. All authors contributed to editing and improving several versions of the manuscript.

Data availability: The authors confirm that the data supporting the findings of this study are available within the article and in Supplementary Material Table S1.

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