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Seasonal dynamics of range expansion in South American thrushes

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Abstract

Background Species ranges are shaped by a variety of ecological and environmental factors that are inherently dynamic, fluctuating in response to climatic, biotic, and anthropogenic influences. Dispersal plays a key role in range shifts, allowing species to adapt to changing habitats and exploit new regions. In this study, we examined the dispersal processes of four thrush species (*Turdus amaurochalinus*, *T. chiguanco*, *T. falcklandii* and *T. rufiventris*) that have expanded their ranges in recent decades, with a focus on the interaction between spread and seasonal movements.

Methods We collected eBird records from 2003 to 2023 to create heat maps that illustrate changes in densities of reported occurrences between seasons and over the years. We also evaluated how bioclimatic and land cover variables influenced the observed variations.

Results The four thrush species have shown significant range expansions, with initially distinct seasonal distributions, which became increasingly similar over time, leading to significant overlap in their breeding and non-breeding habitats. Temperature and precipitation associated with the presence of the four species varied over time and between seasons. Additionally, all four species exhibited shifts in habitat selection, both seasonally and across years.

Conclusion The changes of range are likely driven by a combination of climate and land-use change, and resource availability, which also influence seasonal dispersal patterns. At the same time, thrushes perform very well in urban environments, which offer stable resources and may contribute to their reduction in seasonal movements. Overall, these findings highlight the dynamic nature of thrush species' range shifts and their adaptation to environmental changes.

Keywords Occurrence density, Range expansion, Seasonal patterns, South America, *Turdus*

Background

The range of habitats occupied by a species is shaped by a combination of ecological and environmental features [1]. Most species inhabit complex environments characterized by substantial spatial and temporal heterogeneity. Ongoing climate and land-use changes are expected to render vast areas that were previously suitable for many species no longer adequate, while simultaneously creating new, potentially suitable habitats elsewhere. As a result, the long-term survival of species will rely upon their ability to adapt to these changes by moving across large distances to exploit diverse habitats at various

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spatial scales, allowing them to persist in dynamic and heterogeneous landscapes [2, 3]. Species ranges can vary seasonally [4–6], often in response to fluctuations in food availability and habitat quality [7, 8]. Consequently, movement behavior is closely linked to climatic seasonality and the ability of species to effectively track spatio-temporal variations in resource availability [9, 10].

Some birds find the conditions in their breeding areas favorable enough to remain there year-round. However, for others, conditions once reproductive activity is completed may be more advantageous elsewhere, prompting them to adopt different movement strategies between seasons [11]. Movements at a local scale, in turn, are usually dictated by habitat requirements, feeding needs, and predator avoidance. These movements tend to be concentrated within their territories, where they spend most of their time in areas that offer abundant food, shelter from predators and key locations for displaying and singing [12, 13]. In contrast, dispersal involves movements that are non-directional and non-returning, as birds search for food or suitable nesting sites. These movements can occur between natal sites and subsequent breeding sites (natal dispersal), between consecutive breeding seasons (breeding dispersal), and between wintering sites across different years (non-breeding dispersal), independent of any interim movements [14]. Dispersal plays a crucial role in the redistribution of organisms, gene flow, colonization of new areas, and range shifts [15–17], while also enabling individuals to secure resources, avoid predators, and meet life history requirements.

Species ranges are inherently dynamic and can fluctuate over time in response to climatic, biotic, or anthropogenic variables. When individuals leave familiar territories to colonize new habitats, they face numerous challenges, including unfamiliarity with local resources, pathogens, predators, and disturbance levels [18–20]. Despite these challenges, every year many individuals undertake such movements, exploring new areas far beyond their original territories. These movements can occur through local dispersal, resembling a diffusion-like process, or by long-distance dispersal, which may allow for new geographical areas to be colonized [21, 22], thereby leading to a range expansion [17, 23, 24].

The movements of birds cause their numbers to fluctuate from year to year in specific localities, depending on changes in habitat or food conditions, which in turn affects patterns of abundance and distribution across their range [14]. Understanding these seasonal movements is crucial for elucidating the dynamics of bird distribution and their adaptive strategies in response to environmental changes. In this study, we investigated the history and seasonal dynamics of dispersal of four Neotropical thrush species (*Turdus amaurochalinus*, *T. chiguanco*, *T. falcklandii* and *T. rufiventris*) that are undergoing an expansion in their ranges, with a focus on distinguishing dispersal during breeding and non-breeding seasons.

Methods

Study species

The four studied species occur in different habitats in South America, including forests, scrublands, savannas and also agricultural and urban areas [25, 26]. These species are expanding their ranges, allegedly by taking advantage of the increase in afforestation and urban landscaping [17, 27], with large unoccupied areas in South America representing potential grounds for future colonization [28]. Thrushes are primarily arboreal, relying on trees and shrubs for nesting and food, but also foraging on the ground, mainly on fruits and invertebrates [29]. They breed at various times and locations in South America, from August to April, and their incubation times range from 13 to 16 days, with nestling periods of 10 to 15 days [30–32].

Data gathering and analysis

We looked for daily presence data of each species from 2003 to 2023 at eBird [33], and processed these information using the auk package [34]. Records with no date or location and duplicate occurrences were excluded from the analysis. We filtered the dataset to include only "Stationary" and "Traveling" protocols, those that had a duration of 0–5 h, a distance of between 0 and 5 km, taken by 10 or fewer observers, and "complete" checklists (i.e., all species observed were recorded). These thresholds align with established best practices for processing citizen science data, which emphasize the need to address variability in observation effort and detectability [35]. By filtering datasets in this manner, we aimed to maximize the quality of the records while ensuring spatial and temporal consistency in our analyses. Checklists fulfilling the previous criteria and not mentioning the species of interest were considered pseudo-absences. Based on the dispersal distance reported for other species of the same genus [36, 37], we established a buffer zone of 20 km around each pseudo-absence point. Only latter sightings within these areas were considered as new occurrences, in order to deal with any artificial range expansion linked to an increase in the number or the extension of bird watchers' reports [17]. To further refine our analysis, we performed a spatial thinning using the "ntbox" R package [38], considering only occurrences that were at least 2 km apart from any other record, in order to avoid potentially pervasive effects of sampling bias. The scale of the thinning was selected to achieve a balance between avoiding an over-representation of certain zones due to a higher presence of birdwatchers without sacrificing special resolution relevant to the analysis.

We subsequently divided the occurrence dataset into two seasonal categories: breeding (spring and summer: September to February) and non-breeding (autumn and winter: second-half May to July), based on information about the annual cycles of the species [25, 26, 30–32]. Records corresponding to March, April, first half of May and August were not included in the analysis in order to prevent possible overlapping between breeding and non-breeding seasons. For details about total occurrences and the breakdown across species, seasons and temporal periods see Table 1 and Supplemental Material S1. We subsequently defined three temporal classes, with the first one containing occurrence records grouped in 10-year intervals (2003–2013). Due to the recent increase in records [39], and in order to achieve a clearer visualization, we organized the more recent classes as 5-year intervals (2014–2018 and 2019–2023).

We built heat-maps representing the density of reported occurrences for each species at each season and time frame. The densities were estimated using a kernel density estimation (KDE) method implemented via the kde2d function from the MASS package [40] in R. This approach allows for a smooth representation of occurrence patterns across spatial coordinates, accounting for local clustering while minimizing noise from sparse data points. We created generalized linear models (GLM) using glm function from the base stats package, which is part of the default R installation [41] to test for changes in latitudinal and longitudinal extremes in the distribution of each species between seasons and through the years. Geographic coordinates were included as response variables, and season, year, and their interaction as predictor variables, with a Gaussian error distribution.

To analyze the influence of environmental variables on the range expansions and seasonal movements of the studied species, we used the WorldClim 2.1 Historical Monthly Weather dataset, which includes monthly values for minimum temperature, maximum temperature, and precipitation, available up to the year 2021. For each point, we extracted the corresponding climatic data based on the year and month of observation, ensuring that the climatic conditions accurately reflected the season (breeding and non-breeding) and time period of occurrence. All three variables represent ecological importance since Minimum Temperature is particularly relevant during the non-breeding season, as it represents thermal constraints that may limit the survival or movement of species into colder regions, while Maximum Temperature is critical for the breeding season, as high temperatures can influence food availability and nesting conditions. Conversely, precipitation is a key driver of habitat productivity and water availability, impacting both breeding (e.g., vegetation for nesting) and non-breeding periods (e.g., resource availability in drier months). We also developed GLMs using each bioclimatic variable as a response variable, and year, season and their interaction as predictor variables. We used a Gaussian family for those models including temperature-related variables as response, and gamma family for precipitation variables. The GLMs were evaluated considering both the statistical significance of the coefficients and the overall model fit. Likelihood Ratio Tests were used to assess the contribution of explanatory variables and standardized residuals were checked to identify possible deviations from model assumptions. For the multinomial analysis, specific goodness-of-fit measures, including the evaluation of standardized residuals and Log-Likelihood, were used to determine the quality of the model fit. Finally, we performed a multinomial analysis using multinom function from nnet package [42] to assess how habitat use according to different land cover types from Google Earth Engine varied between seasons and over time. We selected the land cover layer corresponding to the middle year of each interval of years, and grouped all the different subcategories for forests and shrublands into single categories named forests and shrublands, respectively. All the analyses were developed in R [41]. Details about model parameters and confidence intervals are given in Supplemental Material S2.

Table 1 Distribution of the number of data for each species according to season and time period

Species	Period	Season		Total records
		Breeding	Non-breeding	
T. amaurochalinus	2003–2013	263	124	387
	2014–2018	1869	827	2696
	2019–2023	7594	3542	11,136
T. chiguanco	2003–2013	287	149	436
	2014–2018	1009	497	1506
	2019–2023	2903	1582	4485
T. falcklandii	2003–2013	352	81	428
	2014–2018	2076	702	2778
	2019–2023	5292	2411	7703
T. rufiventris	2003–2013	386	154	540
	2014–2018	2333	1141	3474
	2019–2023	7664	3992	11,656

Results

Turdus amaurochalinus showed an overall increase in its range in the last 20 years, evidenced by a significant expansion in its extreme latitude and longitude ($p < 0.01$; Table 2; Fig. 1A). Density of reported occurrences during the breeding season of 2003–2013 was concentrated in two areas, at about 25°S and 35°S (Fig. 1B). Density of reported occurrences looked similar between seasons, except for a third area of high density towards the north, at 20°S, during non-breeding season (Fig. 1B). In 2014–2018, the northern concentration area stopped being

Table 2 Geographical coordinates occupied by four species of neotropical thrushes (*Turdus* spp.) in breeding and non-breeding seasons between 2003 and 2023. The range of latitudinal and longitudinal degrees occupied over the different time periods and the trend and directionality of the range change are shown

			Period	**Media**	**SD**	**Min.**	**Max.**	**Range (degrees)**	**Trend**
Turdus amaurochalinus	Breeding	Latitude	2003–2013	-26.049	6.68	-35.273	-11.014	24	Increase (north and south)
			2014–2018	-27.051	5.878	-40.773	-2.96	38	
			2019–2023	-27.045	6.034	-45.838	-2.833	43	
		Longitude	2003–2013	-56.068	8.154	-71.595	-40.068	32	Increase (west and east)
			2014–2018	-55.175	7.559	-70.706	-35.859	35	
			2019–2023	-55.183	7.505	-72.722	-34.846	38	
	Non-breeding	Latitude	2003–2013	-24.878	6.944	-38.004	-12.355	26	Increase (north and south)
			2014–2018	-26.684	6.141	-45.729	-3.724	42	
			2019–2023	-27.325	5.844	-48.753	-2.567	46	
		Longitude	2003–2013	-57.276	7.785	-71.376	-40.069	31	Increase (west and east)
			2014–2018	-55.622	7.413	-71.376	-38.933	32	
			2019–2023	-55.584	7.297	-72.672	-34.917	38	
Turdus chiguanco	Breeding	Latitude	2003–2013	-16.462	8.677	-42.761	-0.765	42	Increase (south)
			2014–2018	-20.456	10.319	-43.294	-1.000	42	
			2019–2023	-22.144	10.882	-45.836	-0.201	46	
		Longitude	2003–2013	-71.531	4.921	-79.783	-58.060	22	Increase (slightly to the east)
			2014–2018	-69.919	5.026	-79.790	-63.601	16	
			2019–2023	-69.618	4.915	-80.004	-57.934	22	
	Non-breeding	Latitude	2003–2013	-14.103	8.031	-35.743	-1.087	35	Increase (south)
			2014–2018	-19.653	10.139	-42.777	-1.640	41	
			2019–2023	-22.684	10.627	-45.069	-0.069	45	
		Longitude	2003–2013	-72.939	4.891	-79.543	-64.270	15	Increase (slightly to the east)
			2014–2018	-70.457	5.207	-81.234	-63.821	17	
			2019–2023	-69.318	4.823	-79.699	-61.861	18	
Turdus falcklandii	Breeding	Latitude	2003–2013	-39.786	7.693	-55.045	-32.411	23	Increase (north)
			2014–2018	-39.576	6.827	-55.045	-27.067	28	
			2019–2023	-39.877	6.170	-55.101	-26.247	29	
		Longitude	2003–2013	-70.733	2.222	-73.347	-57.763	16	Increase (slightly to the west)
			2014–2018	-71.149	2.168	-74.125	-56.978	17	
			2019–2023	-71.250	2.223	-74.184	-57.536	17	
	Non-breeding	Latitude	2003–2013	-35.853	5.821	-54.837	-32.410	22	Increase (north)
			2014–2018	-36.900	5.812	-54.933	-27.298	28	
			2019–2023	-38.180	5.475	-54.939	-23.635	31	
		Longitude	2003–2013	-71.003	1.431	-73.441	-61.798	12	Increase (west and east)
			2014–2018	-71.215	1.650	-74.104	-57.808	16	
			2019–2023	-71.311	2.011	-74.143	-57.778	16	
Turdus rufiventris	Breeding	Latitude	2003–2013	-26.819	6.757	-38.588	-7.332	31	Increase (north and south)
			2014–2018	-26.782	6.336	-45.837	-3.610	42	
			2019–2023	-27.137	6.366	-48.634	-3.415	45	
		Longitude	2003–2013	-53.522	7.607	-69.308	-38.515	31	Increase (west and east)
			2014–2018	-53.486	7.729	-69.346	-34.882	34	
			2019–2023	-53.929	7.737	-71.192	-34.866	36	
	Non-breeding	Latitude	2003–2013	-26.018	6.207	-37.771	-5.074	33	Increase (north and south)
			2014–2018	-26.672	5.899	-38.607	-3.540	35	
			2019–2023	-27.047	6.171	-42.780	-3.528	39	
		Longitude	2003–2013	-52.560	7.556	-68.872	-39.039	30	Increase (east)
			2014–2018	-53.787	7.541	-68.927	-34.882	34	
			2019–2023	-54.154	7.626	-69.272	-34.832	34	

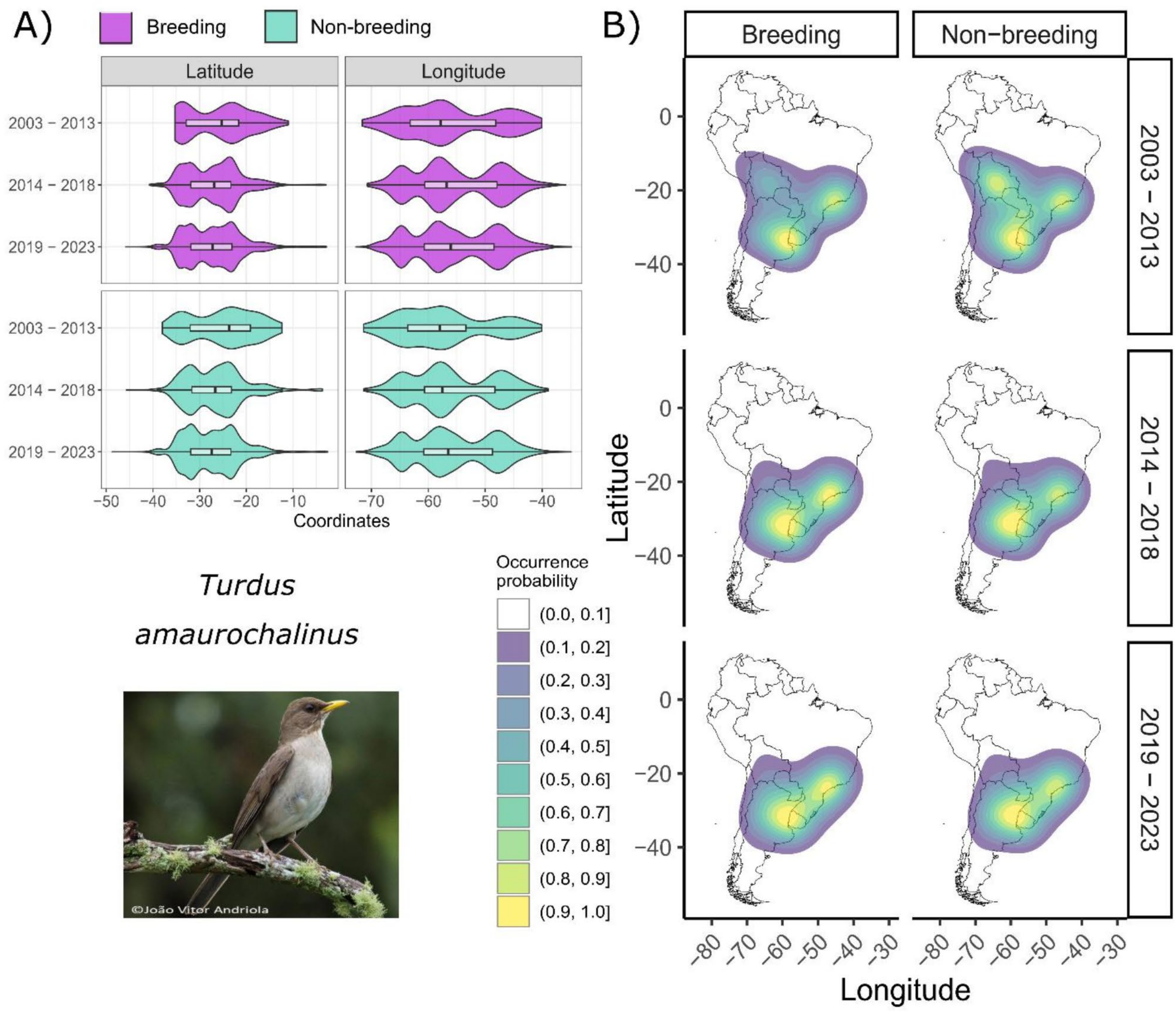

Fig. 1 Distribution of latitudinal and longitudinal coordinates occupied by *T. amaurochalinus* in the different seasons and over time. Panel A: Boxplots represent the median and interquartile range, providing a summary of its central tendency and variability. Surrounding them, the violin plots illustrate the full distribution and density of the data, offering additional insight into its shape and spread. Panel B: Occurrence probability maps modelled by kernel density estimation (KDE) show areas with different probability of species occurrence between seasons and across the years. Parentheses indicate non-included value and brackets indicate included value. Photo extracted from Macaulay Library database, Cornell Lab of Ornithology

evident in non-breeding season (Fig. 1B). Density patterns of reported occurrences in 2019–2023 looked similar to those in the previous period (Fig. 1B). Comparisons revealed initial seasonal movements that were reduced to the point of practically disappearing in the last ten years, with the species then occupying similar habitats all year round (Fig. 1A and B).

We found that temperature values at the sites reported for *T. amaurochalinus* during the breeding season were significantly higher compared with those during the non-breeding season, and these differences became more pronounced over time (Fig. 2; Table 3). For the breeding season, the species moved into locations associated with slightly higher maximum temperatures over time, while during the non-breeding season, temperature-related variables at occurrence points showed a consistent decrease (Fig. 2; Table 3). Regarding precipitation, *T. amaurochalinus* was initially associated with sites experiencing higher precipitation during both seasons, but this trend shifted, with precipitation levels at occurrence points gradually decreasing over the years (Fig. 2; Table 3). The use of different types of habitats differed over time ($p < 0.01$) and between seasons ($p < 0.01$), although the general trends between seasons over time

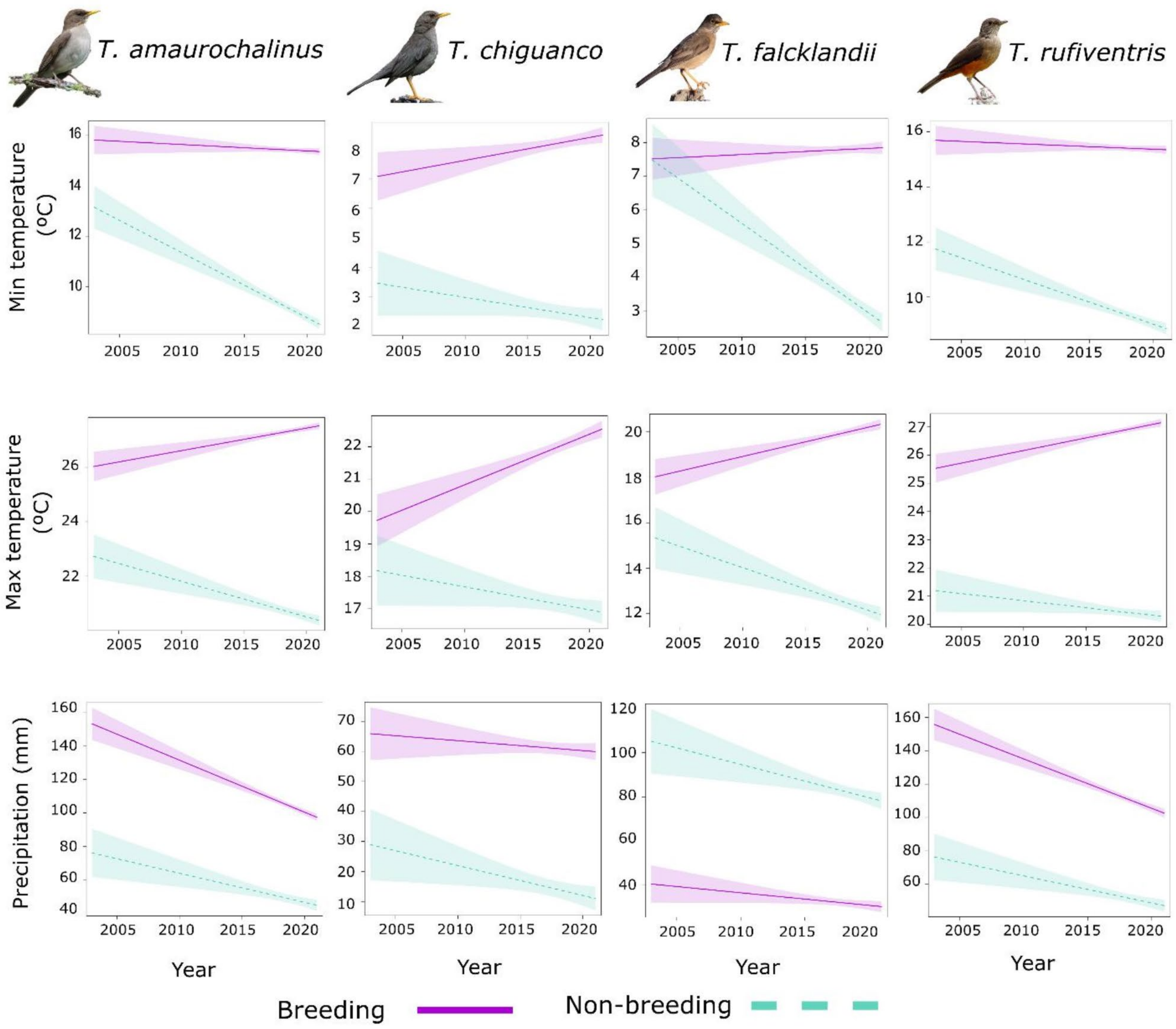

Fig. 2 Changes in the bioclimatic variable values at the occurrence points of the thrushes species over time. Each data point represents the bioclimatic condition at a specific location where the species was observed during the given time period

were similar ($p = 0.49$; Fig. 3A). Over the years, reports of *T. amaurochalinus* were less associated to forest habitats and increasingly to savannas. During the breeding season the use of savannas was higher compared to the non-breeding season, and the opposite happened in urban areas. Grasslands were also important for the species in both seasons (Fig. 3A).

Turdus chiguanco also expanded its range during the studied years, mainly to the south ($p = 0.01$; Table 2; Fig. 4A). During the breeding season of 2003–2013, density of reported occurrences was highest around 15ºS (Fig. 4B). Density distribution during the non-breeding season was similar to the breeding season, with a slightly expanded area of concentration to the north (Fig. 4B). Between 2014 and 2018, a new area of high-density of reported occurrences emerged further south, ca. 30ºS, that persisted throughout the last five years in both seasons (Fig. 4B). Overall, the species initially showed different patterns of seasonal density, with movements of high concentration areas together with a southwards expansion in recent years (Fig. 4A and B).

We found that temperature values at the sites where *T. chiguanco* was reported during the breeding season were significantly higher than those recorded during the non-breeding season (Fig. 2; Table 3). Over time, the species exhibited a trend of occupying locations associated with slightly higher temperatures during the breeding season, while temperature-related variables at occurrence points for the non-breeding season showed a modest decrease over the years (Fig. 2; Table 3). In terms of precipitation,

Table 3 ANOVA results based on generalized linear models (GLMs) evaluating the influence of climatic variables (minimum temperature, maximum temperature, and precipitation) on the seasonal movements of four *Turdus* species. The models included year, season (breeding and non-breeding), and their interaction as predictors. The table reports Chi-square values (Chisq), degrees of freedom (Df), and *p*-values for each variable and factor analyzed. Significant values are highlighted in bold

		T_min			**T_max**			**Precipitation**		
		Chisq	**Df**	***p*-value**	**Chisq**	**Df**	***p*-value**	**Chisq**	**Df**	***p*-value**
T. amaurochalinus	season	5011.4	1	**2.2e-16**	6070.8	1	**2.2e-16**	1353.1	1	**2E-16**
	year	41.5	1	**1.2E-07**	1.3	1	0.245	108.31	1	**2E-16**
	season: year	50.4	1	**1.2E-09**	46.6	1	**8.7E-09**	6.02	1	**0.014**
T. chiguanco	season	1301.3	1	**2.2e-16**	966.25	1	**2.2e-16**	744.1	1	**2.00E-16**
	year	1.33	1	0.249	11.72	1	**0.0006**	5.47	1	**1.90E-02**
	season: year	9.57	1	**0.002**	24.12	1	**9.00E-04**	1.71	1	0.1903
T. falcklandii	season	1437.1	1	**2.2e-16**	2620.4	1	**2.2e-16**	1048.5	1	**2.2e-16**
	year	9.73	1	**0.002**	3.91	1	**0.048**	10.79	1	**1.10E-03**
	season: year	47.99	1	**4.3E-09**	36.27	1	**1.70E-06**	2.75	1	0.097
T. rufiventris	season	4560.2	1	**2.2e-16**	5542.5	1	**2.2e-16**	1372	1	**2.00E-16**
	year	19.5	1	**0.0102**	10.2	1	**0.001**	95.3	1	**2.00E-16**
	season: year	20.5	1	**0.006**	21.7	1	**3.20E-03**	5.7	1	**0.016**

T. chiguanco was initially associated with sites experiencing higher precipitation levels in both seasons. However, this pattern shifted over time, with precipitation levels at occurrence points gradually decreasing in both the breeding and non-breeding seasons (Fig. 2; Table 3). The use of different types of habitats differed over time ($p = 0.01$) and between seasons ($p = 0.02$; Fig. 3B). *Turdus chiguanco* was more prevalent in grasslands areas during both seasons. Over time decreased forest sites occupied by the species and increased the use of shrublands during the breeding season. Savannas were also environments selected by *T. chiguanco* throughout the year. Over years, the use of urban and built-up areas decreased during breeding season and increased during non-breeding season (Fig. 3B).

The expansion of *Turdus falcklandii* was particularly evident during the non-breeding season ($p < 0.01$; Table 2; Fig. 5A). In 2003–2013 greater densities of reported occurrences during the breeding season were found in Andean areas around 35°S with areas of intermediate densities towards the south. In contrast, during the non-breeding season, densities were exclusively concentrated around 35°S (Fig. 5B). In 2014–2018 a range increase during the non-breeding season (Fig. 5A) led to similar inter-seasonal patterns that persisted over the last five years (Fig. 5B). Initially, *T. falcklandii* showed seasonal movements, with high-density areas concentrated in the north of their distribution during the non-breeding season that gradually converged to a similar distribution pattern in both seasons ($p < 0.01$; Fig. 5A and B).

We found that temperature values at the sites where *T. falcklandii* was reported during the breeding season were higher than those recorded during the non-breeding season (Fig. 2; Table 3). Over time, the species displayed a trend of occupying locations associated with slightly higher maximum temperatures during the breeding season, while temperature-related variables at occurrence points for the non-breeding season showed a gradual decrease as the years progressed (Fig. 2; Table 3). Regarding precipitation, *T. falcklandii* was initially associated with sites experiencing higher precipitation levels in both seasons. However, this association shifted over time, with precipitation levels at occurrence points decreasing consistently during both the breeding and non-breeding seasons (Fig. 2; Table 3). The use of different types of habitats by *T. falcklandii* differed over time ($p < 0.01$) and between seasons ($p < 0.01$; Fig. 3C). We found a greater occupation of forests during the breeding season compared to the non-breeding season and an increase in the use of this environment in the last 20 years in both seasons ($p < 0.01$; Fig. 3C). Savannas, grasslands and built-up lands were the next most important habitats for *T. falcklandii*, although the occupancy of the latter has decreased slightly over time in both seasons (Fig. 3C).

Turdus rufiventris showed and overall increase in its range, both latitudinally and longitudinally ($p = 0.04$; Table 2; Fig. 6A). In 2003–2013, high-density areas of reported occurrences were found around 35°S and 20°S during the breeding season. During the non-breeding season, the pattern was similar to that of the breeding season, although the highest values were mainly concentrated in the northernmost area (Fig. 6B). In 2014–2018, densities of reported occurrences were uniform between seasons, and this pattern persisted for the next five years ($p = 0.10$; Fig. 6B). In summary, unlike what was observed for the rest of the species studied, the density distribution of *T. rufiventris* was already homogeneous between seasons since the first period of analysis.

We found that temperature values at the sites where *T. rufiventris* was reported during the breeding season

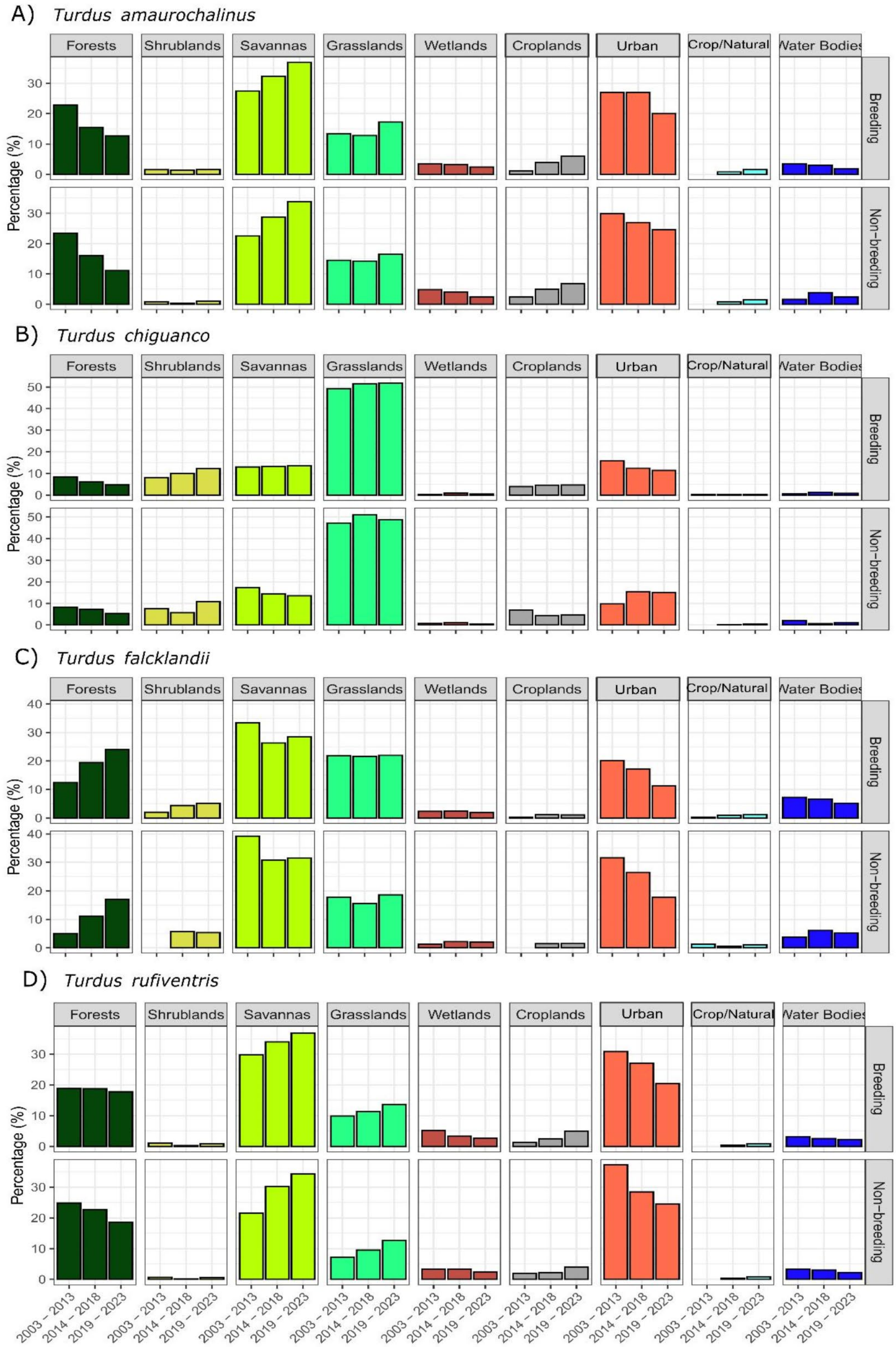

Fig. 3 Land cover types associated to sites used by four species of thrushes (*Turdus* spp.) in breeding and no-breeding seasons from 2003 to 2023

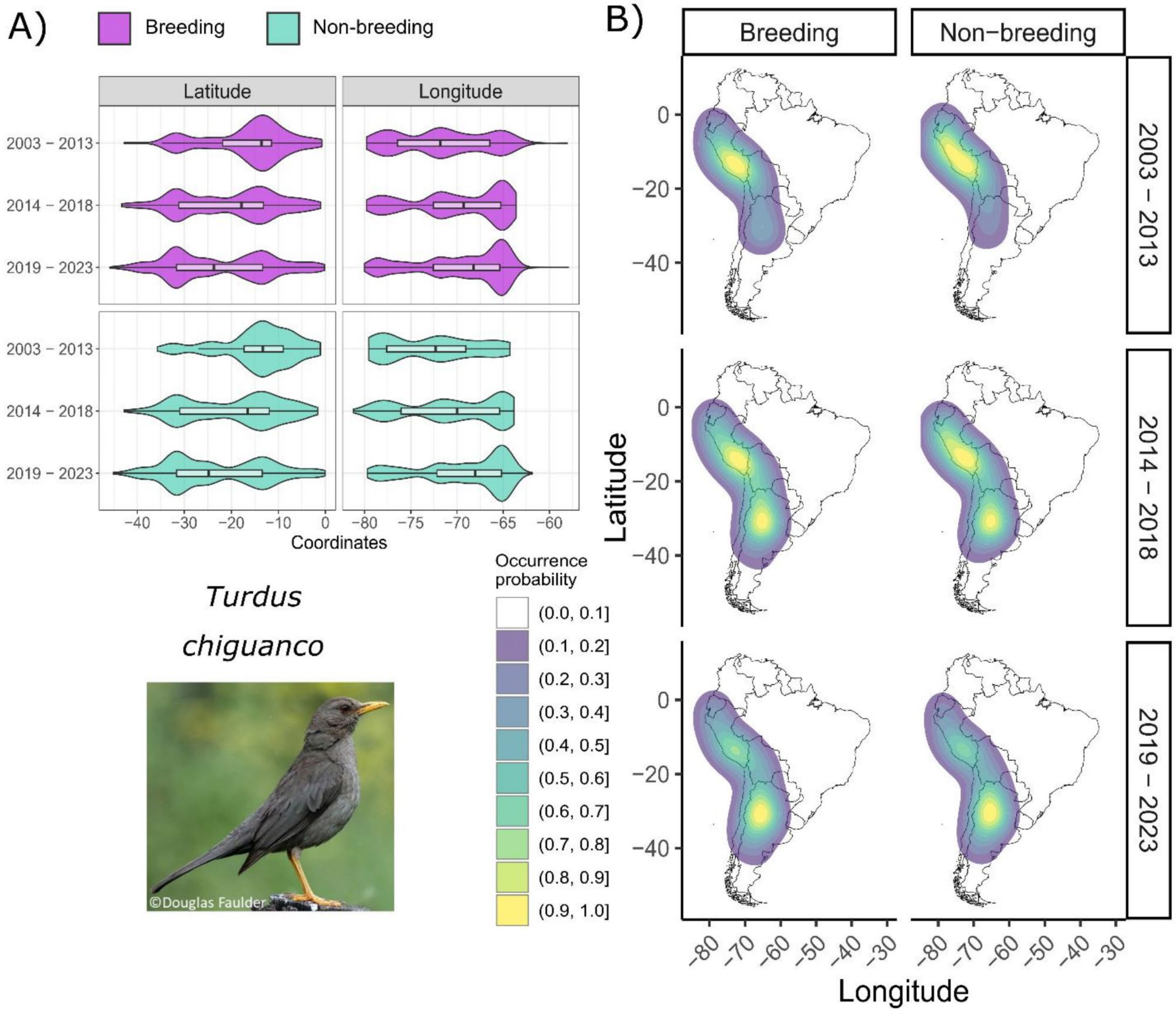

Fig. 4 Distribution of latitudinal and longitudinal coordinates occupied by *T. chiguanco* in the different seasons and over time. Panel A: Boxplots represent the median and interquartile range, providing a summary of its central tendency and variability. Surrounding them, the violin plots illustrate the full distribution and density of the data, offering additional insight into its shape and spread. Panel B: Occurrence probability maps modelled by kernel density estimation (KDE) show areas with different probability of species occurrence between seasons and across the years. Parentheses indicate non-included value and brackets indicate included value. Photo extracted from Macaulay Library database, Cornell Lab of Ornithology

were significantly higher than those recorded during the non-breeding season (Fig. 2; Table 3). Over time, the species exhibited a trend of occupying locations associated with slightly higher maximum temperatures during the breeding season, while temperature-related variables at occurrence points for the non-breeding season showed a consistent decrease as the years went by (Fig. 2; Table 3). Regarding precipitation, *T. rufiventris* was initially associated with sites experiencing higher precipitation levels in both seasons. Over time, this trend changed, with precipitation levels at occurrence points gradually decreasing in both the breeding and non-breeding seasons (Fig. 2; Table 3). The use of different types of habitats differed over time ($p < 0.01$) and between seasons ($p < 0.01$), although the general trends between seasons over time were similar ($p = 0.80$; Fig. 3D). *Turdus rufiventris* showed a greater occupation of forests during the breeding season compared to the non-breeding season, and an increase in the use of savannas and grasslands over the past 20 years in both seasons. Other important habitats used by the species were urban areas, especially during non-breeding season, although the use of these areas has slightly decreased over time in both seasons (Fig. 3D).

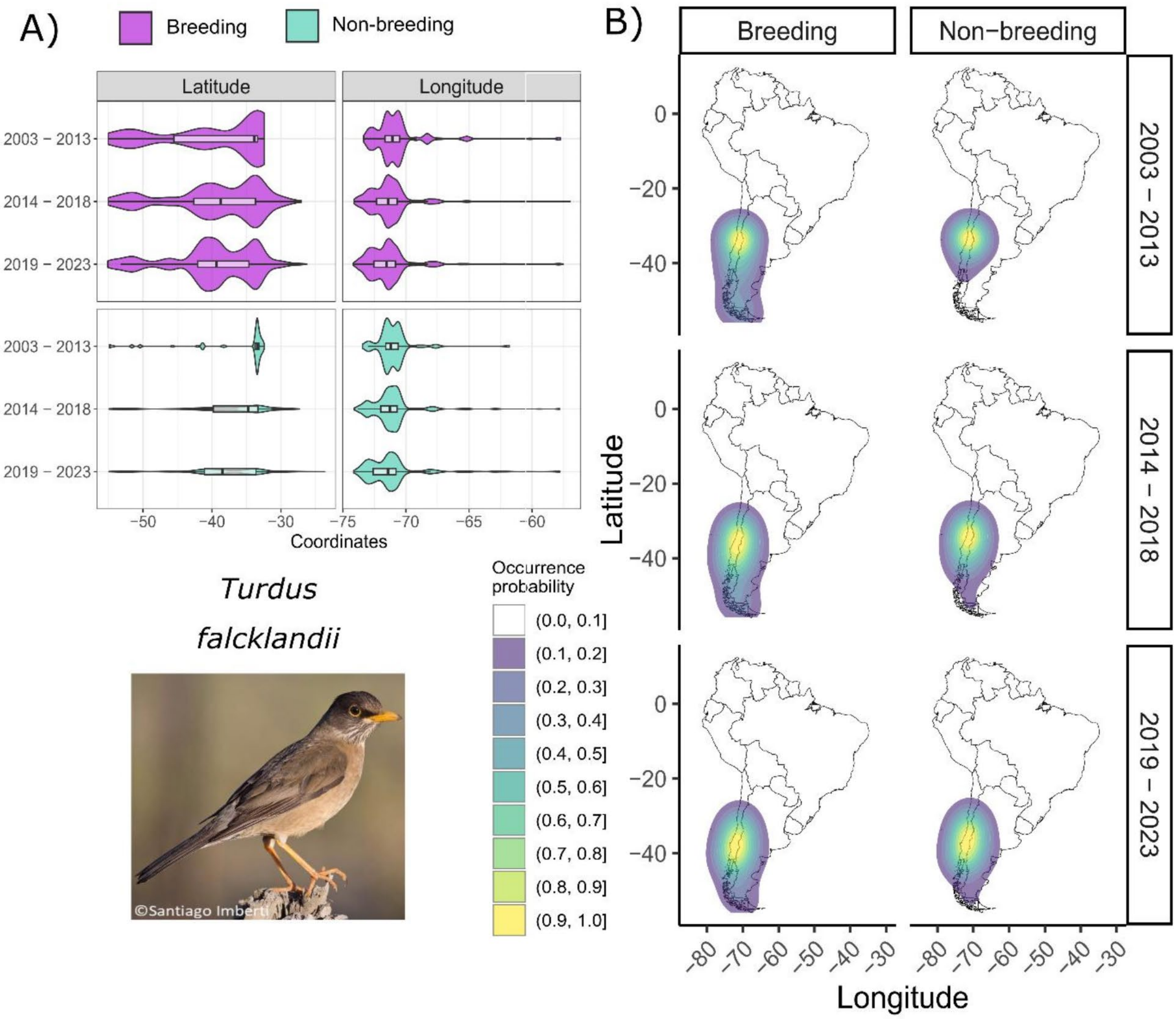

Fig. 5 Distribution of latitudinal and longitudinal coordinates occupied by *T. falcklandii* in the different seasons and over time. Panel A: Boxplots represent the median and interquartile range, providing a summary of its central tendency and variability. Surrounding them, the violin plots illustrate the full distribution and density of the data, offering additional insight into its shape and spread. Panel B: Occurrence probability maps modelled by kernel density estimation (KDE) show areas with different probability of species occurrence between seasons and across the years. Parentheses indicate non-included value and brackets indicate included value. Photo extracted from Macaulay Library database, Cornell Lab of Ornithology

Discussion

Our results confirm the expansion of the distribution areas of the four studied species over the last decades and reveal simultaneous changes in their seasonal movement patterns, offering insights into the dynamics and potential causes of their spread. The analysis revealed an overall range expansion and showed a generalized pattern of convergence between breeding and non-breeding ranges over the past 20 years, though with distinct nuances among the species. For *T. chiguanco* and *T. falcklandii*, there was a notable increase in the area occupied during the non-breeding season. This expansion led to a high overlap with the zones occupied during the breeding season, which were initially more extensive. These results are in line with Lehikoinen, et al. [43] who provided evidence that wildlife responses are seasonally and spatially variable, and can be stronger during the non-breeding season. *Turdus rufiventris* and *T. amaurochalinus* displayed a different pattern. In these species, there were movements of the areas of highest concentration (during the non-breeding season for *T. rufiventris* and in both seasons for *T. amaurochalinus*), leading to overlapping concentration centers throughout the year from the second study period onwards. Notably, in both species, although

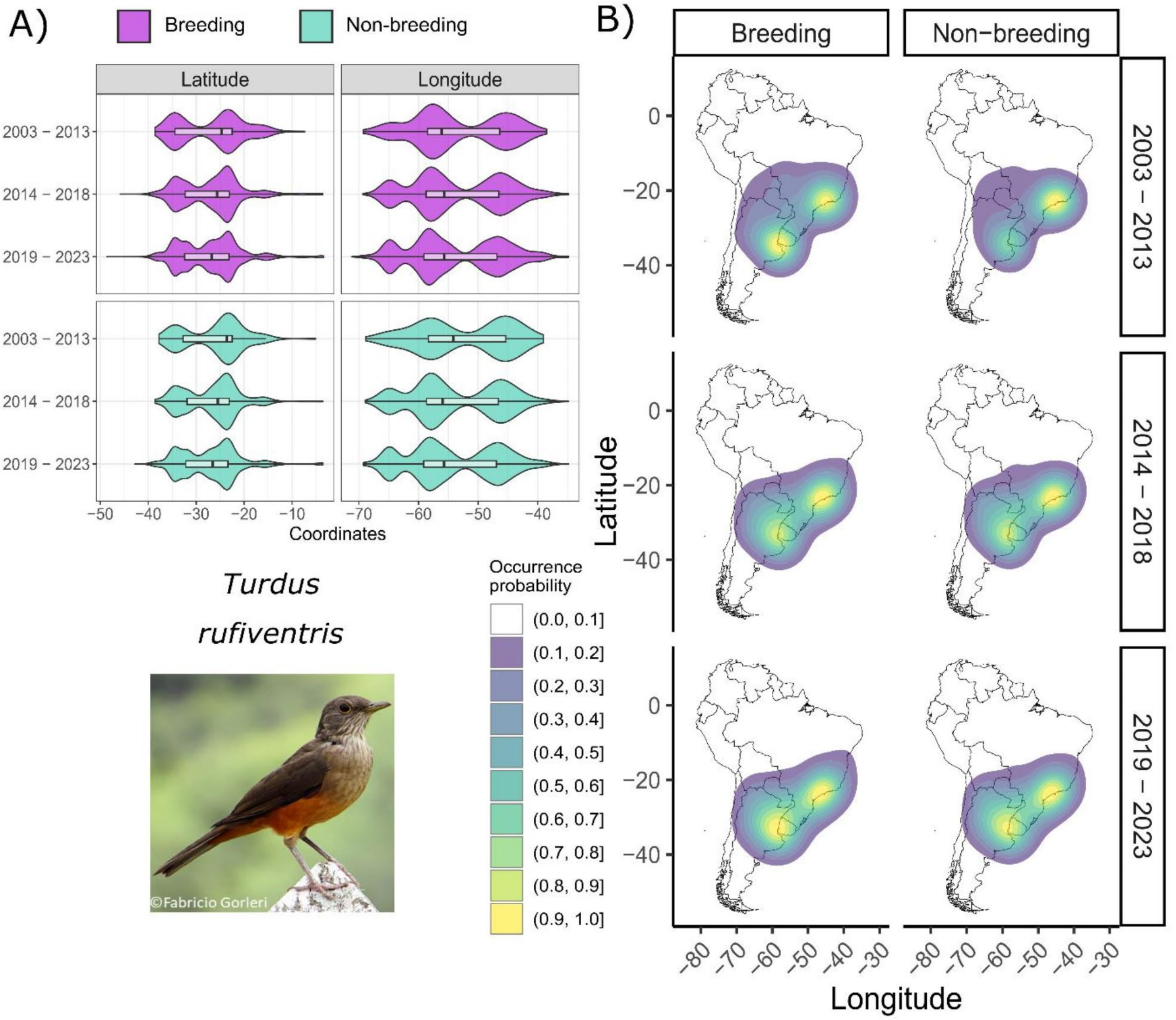

Fig. 6 Distribution of latitudinal and longitudinal coordinates occupied by *T. chiguanco* in the different seasons and over time. Panel A: Boxplots represent the median and interquartile range, providing a summary of its central tendency and variability. Surrounding them, the violin plots illustrate the full distribution and density of the data, offering additional insight into its shape and spread. Panel B: Occurrence probability maps modelled by kernel density estimation (KDE) show areas with different probability of species occurrence between seasons and across the years. Parentheses indicate non-included value and brackets indicate included value. Photo extracted from Macaulay Library database, Cornell Lab of Ornithology

there was a differentiation in the concentration centers, the areas occupied during both seasons were already quite similar from the first study period. This raises the question of whether the seasonal expansion process did not occur in these species or if it started earlier, and by the time of our initial observations, the overlap had already been almost established.

A particularly intriguing pattern is the observed displacement of *T. amaurochalinus* towards the southeast, leaving areas of former higher density of reported occurrences in the northwest, particularly during the non-breeding season. One possible explanation for this displacement is an eventual response to large-scale habitat changes, particularly deforestation and agricultural expansion in its range. The conversion of native forests into soybean plantations, a common land-use change in Paraguay, Bolivia and central and northwestern Argentina since the last decade of the 20th century [44–46], could have reduced the availability of suitable breeding and foraging habitats for *T. amaurochalinus*. In this scenario, the species may be leaving cleared areas towards afforested habitats in the southeast.

The generalized movement patterns we identified align with those observed in the Red-billed leiothrix (*Leiothrix* *lutea*), an exotic passerine in Europe, whose colonization of new areas differed between study periods and seasons [47]. Similar to our findings, the authors detected a range expansion, which was more evident in the non-breeding season, although unlike our results, seasonal movements for *L. lutea* were detected towards the end of the study period. In a complex context of climate and land use changes, it is expected to detect a diversity of change patterns in distribution areas during the reproductive and non-reproductive seasons. In a study in the United States, 68 species of birds shifted their breeding range into regions that historically were cooler and wetter than their original areas of distribution, likely driven by climatic change which affected key parameters of habitat, such as seasonal food availability [48]. In another study, Curley, et al. [49] found that species are shifting their winter centers of abundance also in a manner consistent with the pattern of climate change. In our study we provide evidence that variations in rainfall and temperature could be relevant variables behind changes in seasonal movements and dispersal. Our results, combined with others previously published e.g. [50–52], suggest that range shifts in many species worldwide could similarly be explained by the continuous movement of individuals in response to environmental changes.

Increased temperature, a major contributor to global climate change, is widely recognized as a driver of species range shifts [53, 54]. For those breeding at cold areas, warming likely relax environmental constraints (e.g., vegetation growth, food abundance) and can positively influence breeding success and population growth. For example, increases in the fitness of Dartford warblers (*Sylvia undata*) in the UK [55] and of Eurasian reed warblers (*Acrocephalus scirpaceus*) in Poland [56] has been observed, likely related to a greater availability of breeding habitats due to an amelioration in winter weather severity. Our results suggest that changes in the distribution of thrushes' densities, reflected by the abundance of local reports, may respond to changes in climatic conditions. Temperature and precipitation shifts observed in our results reveal nuanced adaptations of the studied thrush species to changing environmental conditions. For example, the decreasing temperatures at non-breeding sites for *T. amaurochalinus* align with the expectation that milder winters may reduce climatic constraints, facilitating range expansions into previously less favorable areas. Similarly, the trend across all four species to occupy sites with lower precipitation over time suggests an adjustment to drier environments, potentially linked to shifts in habitat availability or resource distribution. These patterns underscore the dynamic interplay between climate variables and habitat preferences, reflecting the ecological flexibility of these species. Local densities may change by an increase in survival associated to less severe winters, as proposed by Maclean, et al. [57] for wader species. Complementary it is expected that an attenuation of extreme winter environmental conditions will also affect seasonal movement patterns, favoring juveniles that choose to remain in the areas in which they were born [43] and eventually leading to an overlap in the distribution areas of the species throughout the year such as that observed in our study. Adjustments exhibited by the studied species highlight how climate-driven changes can alter habitat suitability and influence seasonal movements, ultimately shaping the observed convergence between breeding and non-breeding ranges. This capacity for adaptation not only supports range expansions but also raises questions about the long-term resilience of these species in the face of ongoing climatic and anthropogenic pressures.

The results of our study provide a comprehensive view of the land use and range dynamics of four thrush species over the last two decades. Each species demonstrated distinct yet overlapping patterns of habitat use, reflecting their ecological flexibility and ability to adapt to environmental changes. Forests emerged as an important habitat for all species, particularly during the breeding season. This preference highlights the importance of arboreal environments for nesting, food availability, and predator protection. For instance, *T. falcklandii* showed increases in forest occupancy in both seasons, emphasizing the role of forested areas as stable refuges amidst changing landscapes. This trend suggests that afforestation could play a pivotal role in supporting these species' populations and their range expansion. Environments with more scattered trees, such as savannas and grasslands, were also important habitats for all species. This shift may reflect the suitability of these habitats for foraging and dispersal, as well as potential declines in other habitat types. Notably, *T. amaurochalinus and T. chiguanco* exhibited a reduction in forest use during the breeding season, offset by increased use of savannas and shrublands respectively, which may indicate adaptations to localized habitat changes. Urban areas were relevant for all species, being the second or third most important habitat, although exhibited varying trends. For *T. amaurochalinus*, urban habitat use remained relatively stable but showed a slight decline in recent years. In the case of *T. chiguanco*, its use decreased during the breeding season but increased during the non-breeding season. In contrast, *T. falcklandii* and *T. rufiventris* displayed a slight decrease in urban occupancy. These variations in habitat use exhibited by species could be attributed to habitat saturation or shifts towards alternative habitats offering more favorable conditions.

The convergence of breeding and non-breeding ranges over time across all species is a striking result, underscoring the dynamic interplay between habitat availability, climate, and anthropogenic pressures. This reduction in seasonal differences in habitat use may be driven by the attenuation of climatic extremes as well as the increasing stability of resources in certain environments, such as urban and periurban areas [58]. This trend mirrors patterns observed in other urban-adapted species, such as Eurasian blackcaps (*Sylvia atricapilla*), whose winter ranges have shifted due to the reliable provisioning of food in urban gardens [59]. In the case of *T. falcklandii*, our findings emphasize its higher reliance on forested habitats during the breeding season. This preference likely reflects the advantages these environments provide better nesting sites, microclimatic stability, and protection from predators [60]. However, the role of land-use changes in shaping these patterns cannot be overstated. The conversion of native habitats to agricultural or urban landscapes has likely driven shifts in habitat selection, while afforestation efforts have created new opportunities for colonization. The observed expansion of breeding ranges in *Turdus* species suggests that historical constraints on their distribution may have been linked to the availability of suitable breeding habitats. Afforestation of previously tree-less habitats, like the southern Pampas and the Patagonian steppe may have further facilitated this expansion by creating new suitable habitats that support successful reproduction, thereby accelerating the range expansion seen in these species.

The use of non-forest habitats, such as savannas, grasslands and even urban areas, demonstrates the ecological flexibility of four thrushes studied here. This pattern is consistent with observations in other thrushes, such as *T. viscivorus* in Europe, which has adapted to exploit urban and open habitats for breeding [61]. The ability to utilize a wider range of habitats may facilitate range expansion and reduce dependence on specific seasonal resources, potentially buffering these species against the effects of habitat loss or climate change. Other urbanized bird species are also adapting their annual cycles and seasonal behaviors to exploit urban resources [62]. Thus, the continued availability of local natural surpluses increases the propensity of individuals to turn into sedentary year-round urban and suburban residents [58]. The ecological flexibility of these thrush species has enabled them to exploit a variety of environments, but continued monitoring is essential to understand the long-term implications of these changes.

Beyond the causes underlying the change in the distribution of wild species, and in particular the colonization of new environments, the consequences that this can have on socio-ecological systems are of particular relevance [63]. For instance, birds as seed dispersers influence the temporal and spatial distribution of seeds, with consequences for plant species abundance and community composition [4]. Thrushes are efficient seed dispersers of fleshy-fruited plants, even in urban areas [29]. *Turdus falcklandii* is a primary disperser of plant species in the temperate forests of South America, significantly contributing to the regeneration of native plant communities [64]. However, its movements beyond native forest has led to new interactions aiding the spread of invasive alien plants in its expansion range [65].

While we recognize the limitation of relying on a relatively small set of variables, we believe that focusing on predictors with direct biological relevance to the seasonal dynamics of the studied species (e.g., temperature and precipitation) allows for a meaningful investigation into the drivers of their range shifts. Other mechanisms, such as biotic interactions or changes in resource availability, may contribute to the observed patterns but are beyond the scope of our current dataset. Our study took into account the movements of thrushes throughout their entire annual cycle. Studying seasonal patterns of movement not only sheds light on species' responses to shifting environmental conditions, but also helps to unravel other ecological questions, such as disease transmission [66] or the functional role in the ecosystems, as the case of seed-disperser birds [67, 68]. Dispersal is not a fixed behavior in bird populations and it becomes more and more clear how much it can be influenced by human activities. In this context, our findings have important implications for conservation efforts in the Anthropocene, when rapidly changing environmental conditions mold bird movements and distributions with the subsequent cascade effects on whole ecological communities.

Supplementary Information

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Supplementary Material 1

Supplementary Material 2

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Author contributions
MSV, RR, ALS and SMZ contributed to the study conception and design. MSV led the data curation, RR carried out the analysis. MSV wrote the original draft. All authors read, edited and agreed to the published version of the manuscript.

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Data availability
The datasets used and/or analyzed during the current study are publicly available. The original eBird records used in this study can be accessed

through the eBird data repository at https://ebird.org/data/download?_gl=1*8amdkq*_gcl_au*MTEzOTA3ODY3LjE3MzU2NTg5NjQ.*_ga*MjEwODA1MjU3OS4xNzI2NTE1NzUy*_ga_QR4NVXZ8BM*MTczNzM4MTA4NC4xOC4xLjE3MzczODExMzkuNS4wLjA.&_ga=2.181042151.1597551216.1737381080-2108052579.1726515752, while the bioclimatic datasets from WorldClim used in this analysis are available at https://worldclim.org/data/monthlywth.html#google_vignette. The filtered dataset, used for the analysis of this paper, are available through the public data repository Figshare https://figshare.com/s/8ad00d68b9a3a7bf2cba.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare no competing interests.

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