Changes in bird migration phenology over one century: a perspective from the Neotropical non-breeding grounds

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Summary

Changes in the migration phenology of birds linked to global change are extensively documented. Longitudinal studies from temperate breeding grounds have mostly shown earlier arrivals in the spring and a variety of patterns during fall migration [1,2], yet, no studies have addressed whether and how migration phenology has changed using data from the tropical non-breeding grounds. Understanding whether changes in migratory phenology are also evident in non-breeding sites is essential to determine the underlying causes of

patterns documented in breeding areas. Using data from historical scientific collections and modern repositories of community-science records, we assessed changes in migration phenology of 12 Nearctic-Neotropical long-distance migrant birds in Colombia over one century. We also explored whether shared breeding climatic niches explained variation in changes in phenological patterns observed among species. We detected changes in the timing of both spring and fall migration, with birds generally departing Colombia c. 3 days earlier during the spring and arriving c. 3 days later during the fall, but patterns differed among species in ways not attributable to breeding climatic niches. Our results suggest that birds use cues to time their migration at their non-breeding grounds which are most likely different to those they use on their breeding grounds. To better understand the effects of global change on biodiversity, exploring the underlying drivers of phenological changes with further research integrating more long-term datasets available through scientific collections and community science platforms should be a priority.

Key Words: Community science, long-distance migration, Nearctic-Neotropical migrants, phenological shift, wintering grounds.

Main text (Results and discussion)

We documented a striking phenological shift in the spring and fall migration of birds over more than a century in the Neotropics. By comparing thousands of historical and modern presence records of 12 Nearctic-Neotropical long-distance migratory species in Colombia, we found that in 2009 – 2022, migrant birds arrived at their non-breeding grounds an

average of 3.2 days later in the fall and left their non-breeding grounds in Colombia an average of 3.4 days earlier in the spring compared to 1908 – 1965 (Figure 1A). This change in migration phenology can be described as an "extended summer", with individuals leaving their breeding grounds later in the fall and then returning earlier in the spring. Observing such a shift based on data solely from the non-breeding period is remarkable given the view that cues observable only in the temperate zone (e.g. spring green-up[2]) are thought to largely drive the timing of migratory movements. Our findings thus open an unexplored avenue of research into the mechanisms at work in the tropics to drive phenological changes in migratory birds which breed in the Nearctic.

The magnitude of the overall pattern of an extended summer observed with all records, however, was not common to all species (Figure 1, Suppl. Fig. 1). Blackburnian Warbler (*Setophaga fusca*), Black-and-white Warbler (*Mniotilta varia*), Yellow Warbler (*S. petechia*), and American Redstart (*S. ruticilla*) shared the extended summer pattern with the largest magnitudes of change (Δ = modern - historical; Δ spring = -21.3 days, Δ fall = 29.5 days, Figure 1B). However, Northern Waterthrush (*Parkesia noveboracensis*) and Acadian Flycatcher (*Empidonax virescens*) showed a significant shift in early spring only (Δ spring = -14.1 days, Δ fall = 5.4 days, Figure 1C), while Great-crested Flycatcher (*Myiarchus crinitus*) and Mourning Warbler (*Geothlypis philadelphia*) showed a significant shift in late fall only (Δ spring = -1.7 days, Δ fall = 25.1 days, Figure 1D). Lastly, four species showed no detectable shifts in their migration phenology in either spring or fall: Bay-breasted Warbler (*S. castanea*), Tennessee Warbler (*Leiothlypis peregina*), Summer Tanager (*Piranga rubra*), and Swainson's Thrush (*Catharus ustulatus*) (Δ spring = -2.4 days, Δ fall = -3.7 days, Figure 1E).

Our results, uniquely based on data from the Neotropical non-breeding grounds, are consistent with patterns revealed by studies evaluating phenological shifts in the temperate zone which show evidence of earlier arrivals to the breeding grounds during spring and varying trends for fall departures [3–13]. Aside from a single study including data from the Southern Hemisphere (mainly Australasia) and which highlighted a lack of information from the Neotropics [7], to our knowledge there has been no other research exploring temporal shifts in bird migration phenology from the Neotropical non-breeding period. Recent studies from North America report spring advancements of similar magnitudes to those we observed, albeit in shorter time periods: between 0.5 and 2.9 days per decade for 9 species over 60 years (1961-2018) [11], and a spring advancement of 2.2-2.4 days per decade at a global scale and 0.4 to 1.0 days in North America over 38 years (1978-2016) [8]. Patterns of global change are heterogeneous and thus responses and drivers of change in temperate regions are not necessarily the same as those acting at lower latitudes[4,7]. It is therefore both surprising and enlightening that we find similarities with studies from the temperate zone. Our work is also consistent with prior temperate-zone studies revealing that phenological shifts in migration vary among species [3,5,6], which raises questions about the mechanisms at work within the Neotropics that may drive such changes in different species and populations [7,14].

We hypothesized that species with similar patterns of phenological shift might be responding similarly to common environmental cues for breeding and migration[15] owing to them potentially sharing breeding climatic niches. If this were the case, then we would expect that species sharing phenological shift patterns would also show a high degree of overlap in their breeding climatic niche compared to the niche overlap between species

with different phenological patterns. Species sharing the extended summer pattern had the highest mean overlap in breeding climatic niche (mean D = 0.63 ± 0.06 SD, n = 6 comparisons, 4 spp), but niche overlap was relatively low for species which showed no shift in migration phenology (mean D = 0.36 ± 0.12, n = 6 comparisons, 4 spp), species with a shift only in the fall (D = 0.27, n = 1 comparison, 2 spp), and species with a shift only in spring (D = 0.03, n = 1 comparison, 2 spp) (Figure 2A, Table 1, Suppl. Fig. 2). Differences in niche overlap between species sharing (mean D = 0.45) and not sharing (mean D = 0.43) phenological patterns were not significant (p = 0.552, Figure 2B, Suppl. Table 1). This suggests that conditions at the breeding grounds by themselves do not accurately predict shifts in migration phenology from the non-breeding grounds, at least when measured at this scale and resolution.

Both cue-driven environmental mechanisms (e.g. temperature, precipitation, photoperiod, vegetation greening) and response-driven organismal mechanisms (e.g. trophic level, migratory strategy, ecological specialization) which vary among species, may underlie phenological shifts [16–19]. However, the cues to which migratory birds respond on their non-breeding grounds likely differ from those acting on the breeding grounds [7], particularly when these areas are distant. In North America, temperature appears to be the main cue-driven mechanism underlying shifts in spring arrivals and fall departures [9–11]. Because seasonal temperature variation in northern South America is minimal, changes in temperature are unlikely drivers of the patterns we observed. Alternatively, changes in precipitation cycles may provide tangible cues to drive phenological shifts in migration to and from the Neotropical non-breeding grounds [7,20]. Regular rain and drought cycles, as well as precipitation fluctuations associated with climatic phenomena such as El Niño and

La Niña can drastically affect resource availability in the tropics [21–23], and migratory birds respond to variation in precipitation on their non-breeding grounds by modifying their migration schedules [24–27].

Whether precipitation on the non-breeding grounds in turn relates to temperature or other environmental conditions on the breeding-grounds is not well understood, and how landbirds may shift their cue perception as their migration advances needs more study [28,29]. We are unaware of research on organismal-driven cues (e.g. social foraging cues, individual breeding condition) potentially acting in the tropics and which may also be influencing phenological shifts in migration [7]. Furthermore, the 12 species we analyzed in this study were those with enough historical data to allow meaningful comparisons across time, yet the patterns we uncovered are likely more general given that phenological shifts in migration have been detected in a broad range of Nearctic-Neotropical migratory species [11]. There is a broad and wide-open research avenue exploring how migratory species, populations and individuals respond to environmental and organismal cues throughout their annual cycle and whether these responses translate into adaptation to global change [31], or to increases in phenological mismatches [32,33].

Long-distance Nearctic-Neotropical migratory birds are responding to climate and global change by shifting their fall and spring migration schedules, both on the breeding [8,10,11] and non-breeding grounds (this study). Yet, the persistent and steep population declines of Nearctic Neotropical long-distance migrants [34] and the broad range of responses to global change in different species, suggest that neither plasticity or adaptability may be quick enough or uniform among species to respond to the rising pressures posed by a rapidly changing world [8,19,32,33]. Phenological shifts in migration can accentuate mismatches

between arrivals, departures, and resource peaks that migrants depend on during different periods of their annual cycle [32,35–37]. The fitness and demographic consequences of such mismatches could be devastating to certain populations[36].

Our study highlights the potential to address questions on a global scale by incorporating data from multiple sources. Biological collections provide a snapshot of biodiversity at specific times and locations and, thus, allow tracking of changes dating back decades or even centuries. However, sampling is not uniform across time or geographical locations. Multiple studies addressing changes in migration phenology in birds have been possible due to long-term monitoring through bird banding and standardized surveys. Such datasets are often limited in many tropical regions due to insufficient or poorly documented long-term biodiversity monitoring efforts. The growing popularity and usage of community science platforms have dramatically increased the accessibility to data that would otherwise have required extensive effort and resources to be obtained[38]. These data have proven sufficient to detect patterns over a wide diversity of timescales and geographic ranges[39]. Despite differences in the amount of data obtainable between biological collections and citizen science platforms, our results show how both sources of data can complement each other. We point out yet again, the importance of a more complete understanding of the annual cycle of migratory organisms [40,41], where events occurring on the non-breeding grounds and Neotropical stopover sites are also affecting the phenological dynamics of migration.

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Author contributions

CDC and CG designed the study. DAG, BMA and CG compiled and analyzed the data. All authors contributed to result interpretation and manuscript writing.

Declaration of interests

Authors declare no competing interests.

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Figure legends

Figure 1. Phenological patterns comparing historical and modern data of 12 Nearctic-Neotropical long-distance migratory bird species. Difference between modern and historical records follows: Δ = modern - historical. Thus, negative values indicate current earlier dates and positive values indicate current later dates. A) overall pattern including all species (Δ spring = -3.6, Δ fall = 3.1); B) extended summer (i.e., species currently leave the breeding grounds earlier and arrive later; Δ spring = -21.3, Δ fall = 29.5); C) early spring departure (Δ spring = -14.1, Δ fall = 5.4); D) early fall arrival (Δ spring = -1.7, Δ fall = 25.1); E) no shift (Δ spring = -2.4, Δ fall = -3.7).

Figure 2. A. Niche overlap of the 12 Nearctic-Neotropical long-distance migratory bird species per phenological category. Species sharing the "extended summer" phenological category share most of their ecological niche (mean D = 0.63 ± 0.06 SD, n = 6 comparisons, 4 spp), followed by species which showed no shift in migration phenology (mean D = 0.36 ± 0.12, n = 6 comparisons, 4 spp), only a shift in spring (D = 0.27, n = 1 comparison, 2 spp), and finally species with a shift only in the fall (D = 0.03, n = 1 comparison, 2 spp). B. Comparisons of niche overlap between species sharing phenological shifts (intra-group) and those not sharing them (inter-group) did not show significant differences (p = 0.55).

Figures

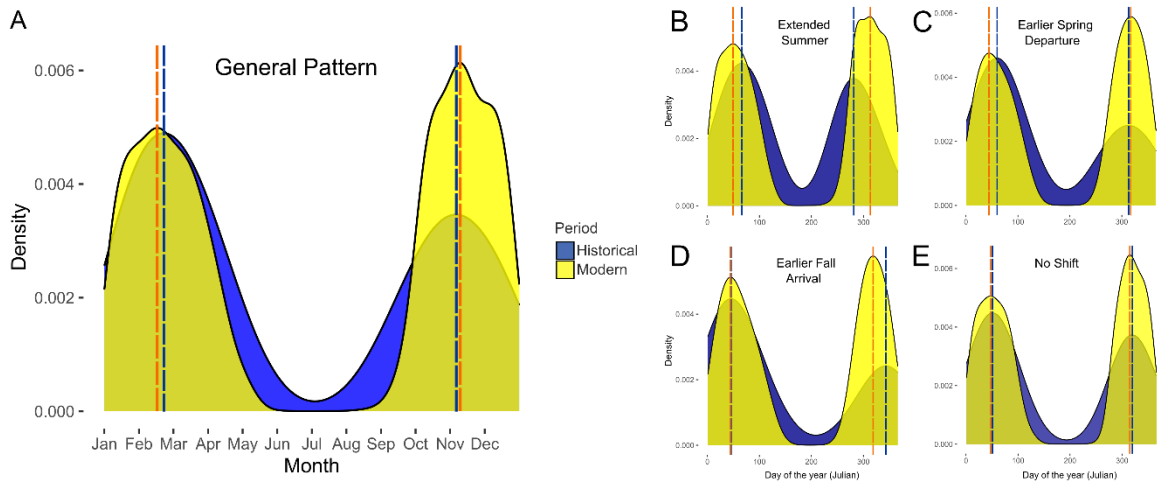


Figure 1.

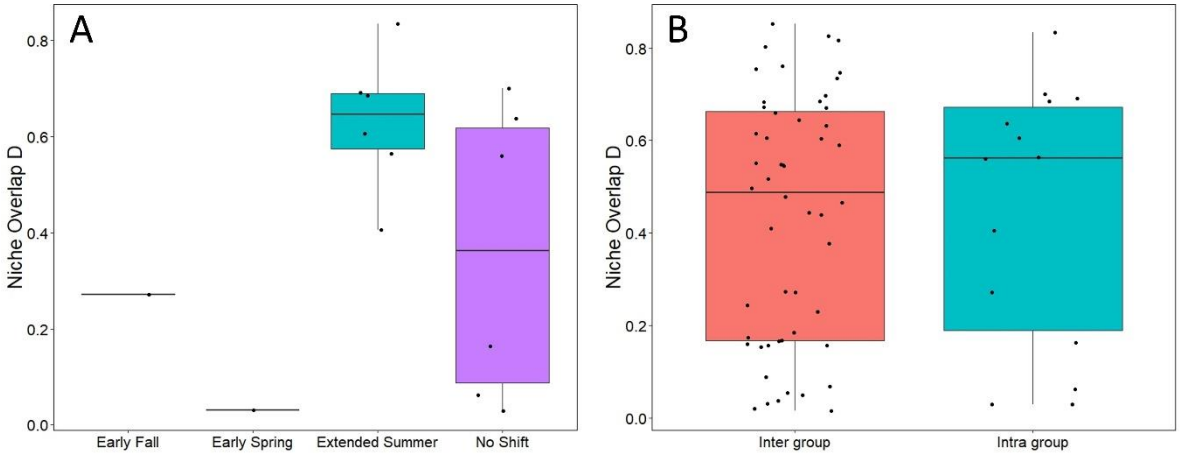


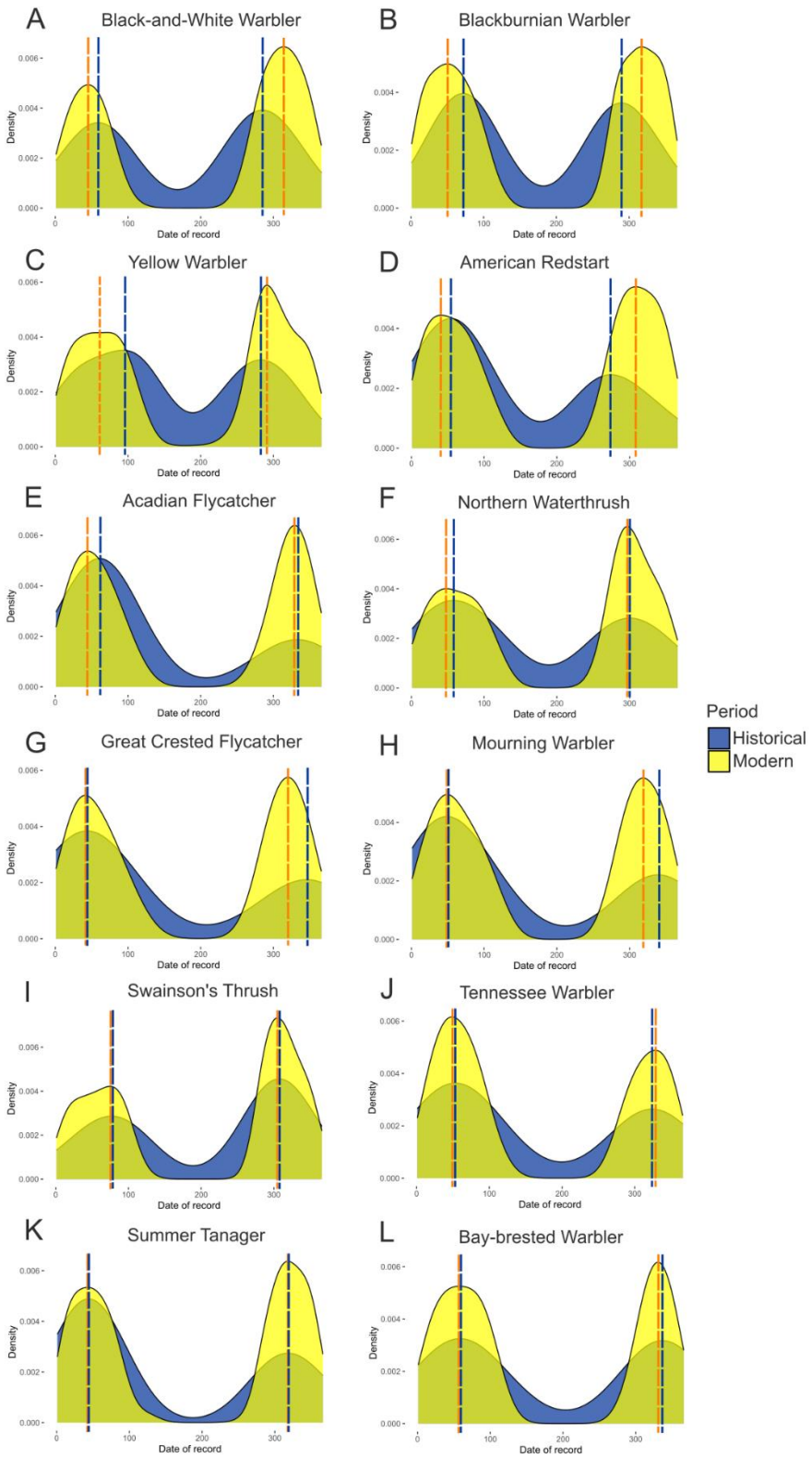
Figure 2.

Tables

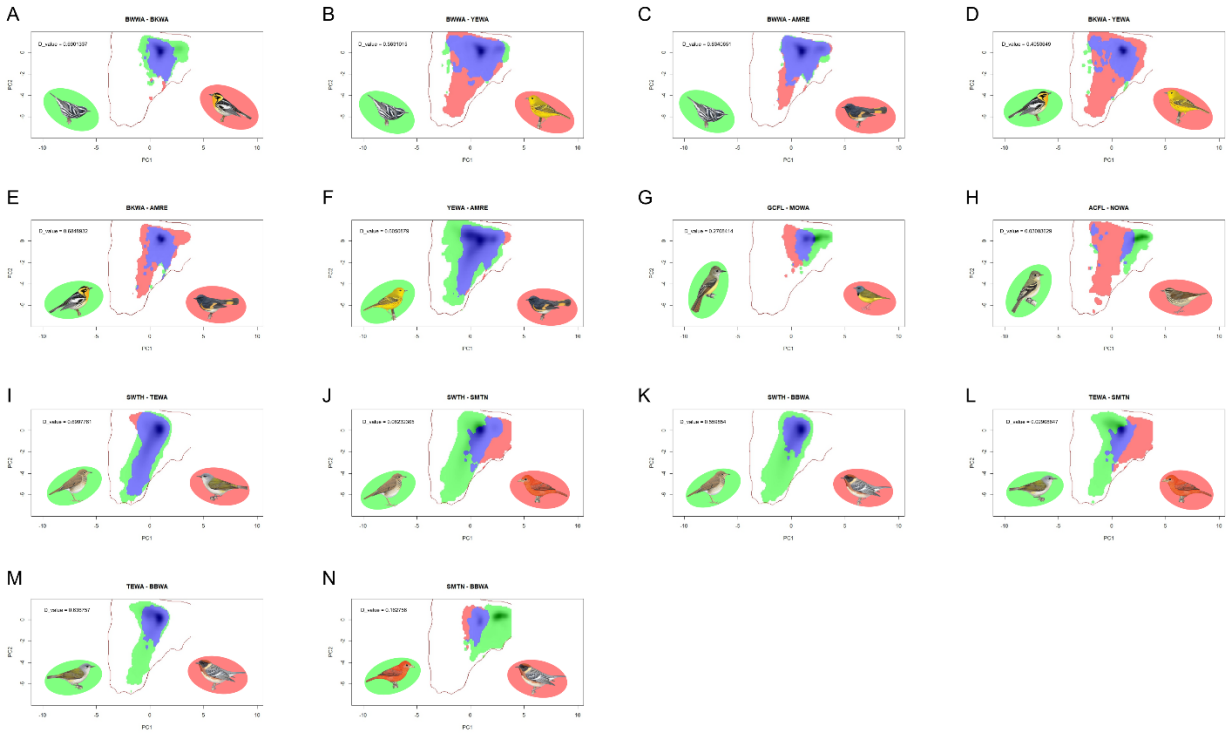
Species	Number of Historical Data	Number of Modern Data	Species Comparisons (D_value)	Phenological Category
Black-and-White Warbler (BWWA)	55	21,357	BKWA (0.69); YEWA (0.56); AMRE (0.83)	Extended Summer
Blackburnian Warbler (BKWA)	76	85,129	YEWA (0.40); AMRE (0.68)	Extended Summer
Yellow Warbler (YEWA)	109	32,077	AMRE (0.60)	Extended Summer
American Redstart (AMRE)	65	20,216	-	Extended Summer
Acadian Flycatcher (ACFL)	51	12,502	NOWA (0.03)	Earlier Spring Departure
Northern Waterthrush (NOWA)	67	13,809	-	Earlier Spring Departure
Great Crested Flycatcher (GCFL)	50	5,136	MOWA (0.27)	Earlier Fall Arrival
Mourning Warbler (MOWA)	63	9,725	-	Earlier Fall Arrival
Swainson's Thrush (SWTH)	70	38,921	TEWA (0.70); SMTN (0.06); BBWA (0.56)	No Shift
Tennessee Warbler (TEWA)	51	14,617	SMTN (0.03); BBWA (0.64)	No Shift
Summer Tanager (SMTN)	157	63,269	BBWA (0.16)	No Shift
Bay-brested Warbler (BBWA)	62	16,309	-	No Shift

Table 1. Ecological niche (D value) comparisons between species that shared the same phenological category (i.e., Extended Summer, Earlier Spring Departure, Earlier Fall Arrival, and No Shift) and number of historical and modern data. Notice that species common names abrebations are used in the "Species Comparisons (D_value)" columbs to show the shared niche between species.

Supplementary materials



Supplementary Figure 1. Individual phenological change graphs for each of the 12 Nearctic-Neotropical long-distance migratory birds. Extended Summer: A) Black-and-white Warbler, B) Blackburnian Warbler, C) Yellow Warbler, D) American Redstart; Early Spring Departure: E) Acadian Flycatcher, F) Northern Waterthrush; Early Fall Arrival: G) Great Crested Flycatcher, H) Mourning Warbler; No Shift: I) Swainson's Thrush, J) Tennessee Warbler, K) Summer Tanager, L) Bay-breasted Warbler.



Supplementary Figure 2. Climatic niche overlap between species that shared their phenological category. Extended summer (A – F), Early Fall Arrival (G), Early Spring Departure (H), and No Shift (I – N). Niche overlap D values for each comparison shown in each box.

Supplementary Table 1. Values of niche overlap (D) estimated for all pairs of species in this study.

	Group	BWWA	BKWA	YEWA	AMRE	ACFL	NOWA	GCFL	MOWA	SWTH	TEWA	SMTN	BBWA
BWWA	Extended Summer	1.00	0.69	0.56	0.83	0.24	0.55	0.41	0.75	0.55	0.61	0.23	0.67
BKWA	Extended Summer		1.00	0.41	0.68	0.09	0.44	0.27	0.83	0.47	0.50	0.07	0.73
YEWA	Extended Summer			1.00	0.61	0.17	0.76	0.27	0.48	0.67	0.68	0.16	0.44
AMRE	Extended Summer				1.00	0.18	0.59	0.38	0.75	0.64	0.66	0.16	0.63
ACFL	Early Spring					1.00	0.03	0.70	0.05	0.03	0.02	0.82	0.02
NOWA	Early Spring						1.00	0.16	0.52	0.68	0.85	0.04	0.55
GCFL	Early Fall							1.00	0.27	0.17	0.15	0.61	0.17
MOWA	Early Fall								1.00	0.55	0.60	0.05	0.80
SWTH	No Shift									1.00	0.70	0.06	0.56
TEWA	No Shift										1.00	0.03	0.64
SMTN	No Shift											1.00	0.16
BBWA	No Shift												1.00

STAR Methods

Resource availability

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Material availability: https://github.com/camilgomo/Fenologia-de-la-migracion-en-Colombia

Data and code availability: https://github.com/camilgomo/Fenologia-de-la-migracion-en-Colombia

Method details

Historical and modern data

We compiled all known historical records of Neotropical migratory birds in Colombia between 1908 and 1965 obtained from public data repositories of scientific collections (dataset available from GitHub). Our complete historical database comprised information for 2455 specimens of 99 species from 31 scientific collections worldwide. For every

record we verified species, date, locality, and geographic coordinates by accessing the original collection records [42]. For the individual species comparisons, we selected species that had complete historical records for at least 50 individuals and removed austral migrants and species with both resident and migratory populations in Colombia due to potential ambiguity in their identification (e.g. *Vireo olivaceus, Tyrannus savana*). This reduced the historical dataset to 876 individuals of 12 species (dataset available from GitHub).

We used the global community science platform eBird [43] to obtain contemporary records of Neotropical migratory birds in Colombia between 2009 and 2022, for all Nearctic Neotropical migrants that winter or fly through Colombia, and also for just the 12 species selected above in our historical dataset. After filtering for verified records, we gathered a total of 333,068 observations.

Exploration of potential biases in historical and modern datasets

We wanted to make sure that any patterns we observed in the migration phenology were not a result of temporal or spatial biases inherent to our datasets. We therefore explored whether there were temporal and spatial biases by plotting the availability of records by month and by latitude and longitude. We did this both for the complete datasets, and for individual species. Neither the historical nor the modern datasets showed temporal or spatial biases, so we continued with our analyses as described below.

Comparison of historical and modern migration phenology

We constructed density plots of migration phenology for the historical and modern datasets, both for all species together and for each species individually. We overlapped historical and modern phenology plots and determined the date of maximum density of migrants in

Colombia during spring (peak abundance between March and May) and fall migration (peak abundance during September and November) by calculating the local maximum for each period. To determine whether there were significant differences between historical and modern local maxima, we estimated the observed difference between historical and current local maxima dates in spring and fall migration. We then randomized the period of our data (e.g. historical, or modern) and estimated the new differences for 999 iterations. P values were obtained by comparing our observed difference to the randomized distribution. We considered the day of maximum density to be a reliable metric of the general phenological pattern of a species [44]. All analyses were carried out in R [45] and all code and data are available from GitHub (https://github.com/camilgomo/Fenologia-de-la-migracion-en-Colombia).

Breeding climatic niche overlap for species sharing phenological shift patterns

We used the R package ecospat [46] to estimate climatic niche overlap values for species which shared phenological patterns of migration shift in four categories based on the trends of the day of maximum density between historic and modern data: 1) extended summer (earlier spring departure and later fall arrival to the non-breeding grounds), 2) early spring (earlier spring departure from the non-breeding grounds and no change during the fall), 3) early fall (no large changes during the spring and earlier arrival to the non-breeding grounds during the fall) and 4) no shift.

We compiled monthly climatic variables for the breeding period (June – August) using Worldclim data [47]. Seven climatic variables were selected based on low autocorrelation criteria, and because they have been shown to describe well Neotropical migratory bird climatic niches [15], elevation, aspect, slope, maximum temperature, minimum temperature,

precipitation seasonality, and temperature seasonality. Current breeding distributions for all species were obtained from eBird Status and Trends [48,49] by selecting the specific weeks that correspond to the breeding period for our target species. We then filtered breeding locations with a probability of occurrence of the species ≥ 50% and then threw 5000 random points over them to get the presence xy coordinates for each species. Random breeding distribution coordinates were used to extract climate values for each species, and an additional 10000 random points were used to extract climatic background values for the whole of North America.

Following Broennimann et al. [46,50] we conducted a multivariate comparison of climatic niche overlap between species which shared phenological shifts in historical and modern migration patterns. Climatic niche overlap is measured using Warren's D statistic which varies from 0 (no climatic niche overlap), to 1 (climatic niches are exactly the same) [15,50]. We compared values of niche overlap between species sharing the same phenological pattern (intra-group) and those not sharing them (inter-group). A randomization of these comparisons, like the one described above, was used to assess significance between the observed differences between groups. All data and code are available form GitHub (https://github.com/camilgomo/Fenologia-de-la-migracion-en-Colombia)

Key resources table

RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Raw historical records of Neotropical migratory birds recorded in Colombia between 1908 - 1965	Gbiff, VertNet, Conservation International Colombia	https://www.gbif.org/ http://www.vertnet.org/
Processed historical dataset of Neotropical migratory birds recorded in Colombia 1908 - 1965	This study	GitHub
Raw modern observation records of Neotropical migratory birds in Colombia 2009-2022	eBird	https://ebird.org/
Processed modern dataset of Neotropical migratory birds in Colombia 2009-2022	This study	GitHub
Breeding distribution rasters of neotropical migrants	eBird Status and trends	https://science.ebird.org/es/status-and-trends/download-data
Coordinates for climatic niche overlap	This study	GitHub
Monthly climatic variables	Worldclim	https://www.worldclim.org/
Other		

R Code and data for migration phenology comparisons	This study	GitHub
R Code and data for climatic niche overlap comparisons	This study	GitHub