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RESEARCH

Century-long shifts in body size and proportions of lowland rainforest birds

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Abstract
Climate change is having profound impacts on biodiversity, with notable effects on the distribution, and morphology of species. Many studies have documented changes in body size and shape in response to changing climatic conditions, with a widespread trend of decreasing body size observed in temperate regions. Despite the growing body of evidence on morphological changes in birds associated with climate change, no study has assessed temporal trends in body size and shape over a century in tropical lowland areas. Using data from museum specimens, we examined morphological trends of 23 bird species in Barbacoas, Nariño, a lowland site near the Pacific coast of Colombia, over the past 109 years. Our results revealed mixed trends in body size. Hummingbirds exhibited an overall decrease in body size, with strong evidence of reduction in *Florisuga mellivora* (White-necked Jacobin). In contrast, non-hummingbirds showed an average increase in body size, with strong evidence of increases in three species: *Microbates cinereiventris* (Tawny-faced Gnatwren), *Myiobius barbatus* (Whiskered flycatcher), and *Myrmotherula pacifica* (Pacific Antwren); and a notable decrease in *Sporophila nigricollis* (Yellow-bellied Seedeater). Wing length decreased across most species, while tail length increased in 61% of them (average increase of 4.4%), possibly in response to changes in forest structure associated with climate change. Changes in bill morphology were limited to an increase in maxilla depth for ten species, with no consistent changes in total bill length, width, or maxilla area. These results underscore the complexity of morphological responses potentially linked to climate change and the need for continued research to understand the factors and mechanisms driving these changes, particularly in tropical bird communities.

Keywords Climate change · Chocó · Long-term trends · Neotropics · Phenotypic accommodation · Resurveys

The Spanish translation of the paper is available in the Supplementary Information. Springer Nature did not copy edit this.

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Introduction

Anthropogenic climate change has become a powerful driver of ecological and evolutionary responses, from shifts in species distributions and phenology that reshape communities (Visser and Both 2005; Durant et al. 2007; Malhi et al. 2020; Neate-Clegg et al. 2024a) to alterations in species' morphology (Tian and Benton 2020). Among these responses, changes in body size and shape have emerged as potentially important responses to warming temperatures. Morphological changes can result from both evolutionary processes and phenotypic plasticity via various mechanisms including the heat exchange hypothesis which predicts that smaller bodies dissipate heat more efficiently, thereby enhancing their ability to cope with warming conditions (Brown and Lee 1969; Gardner et al. 2019). Additional morphological responses to climate change include changes in heat-dissipating appendages, such as tarsi or bills, where larger appendages facilitate heat loss (Allen 1877; Greenberg et al. 2012; Tattersall et al. 2017), though differences in blood flow regulation suggest bills may be more responsive to temperature changes than tarsi (McQueen et al. 2023; Krugler et al. 2025). In addition, in lowland tropical rainforests, high ambient humidity may result in wet bulb temperatures that inhibit evaporative cooling efficiency, potentially increasing reliance on non-evaporative heat dissipation (Gerson et al. 2014; Pollock et al. 2021). Beyond adaptations to heat stress, changes in body size and shape reflecting phenotypic plasticity and evolutionary changes may also be indirectly driven by climate change through alterations in habitat structure (Lurgi et al. 2012), resource availability (Yom-Tov and Geffen 2011; Tan et al. 2021; Dias et al. 2025), and species interactions (Gibert and DeLong 2014). In birds, recent studies have documented complex and sometimes contradictory patterns of morphological change through time (Goodman et al. 2012; Gardner et al. 2014; Kenneth et al. 2020). However, our understanding of these responses remains biased, as most studies have been conducted in temperate regions and on migratory birds (Van Buskirk et al. 2010; Weeks et al. 2020; Dias et al. 2025). This bias is particularly concerning given that tropical ecosystems harbor the majority of Earth's biodiversity and may be especially vulnerable to climate change due to species' narrow thermal tolerances and limited dispersal ability (Janzen 1967; Moore et al. 2008; Sunday et al. 2014). Whether and how tropical species may respond to changing climate adaptively or through plasticity requires additional study.

Recent evidence suggests that the impacts of climate change are not uniform across ecosystems and species. For instance, tropical and temperate shorebirds have shown different morphological responses to climate change (e.g. McQueen et al. 2024). Even within the tropics, studies have revealed contrasting patterns. In Central Amazonia, Jirinec et al. (2021) documented a ~ 7.2% decline in body mass over 40 years (1.8% per decade) across 36 species. In contrast, Neate-Clegg et al. (2024b) found systematic increases in body mass among understory montane birds in Tanzania, with species showing an average 4.1% increase in body mass over 36 years (1.1% per decade). These opposing trends between lowland and montane ecosystems suggest that local environment conditions, such as temperature variability, resource availability, or habitat structure, likely mediate morphological responses to climate warming (Ocampo-Peñuela 2024). However, long-term data from tropical regions remain scarce, particularly from relatively undisturbed lowland rainforests, where species may face unique selective pressures. Expanding research in tropical regions is necessary to provide a clearer picture of possible biogeographical patterns of morphological change in birds associated with climate change.

Long-term datasets spanning more than a century are exceptionally rare in tropical regions, limiting our understanding of responses to environmental change, including morphological shifts. The Colombia Resurvey Project addresses this gap by systematically sampling localities that were originally surveyed by the American Museum of Natural History (AMNH) during their pioneering expeditions of 1910–1915 (Chapman 1917) to study evolutionary and ecological changes in birds (Kattan et al. 2016; Gómez et al. 2022). In October 2021, as part of this initiative, our team re-surveyed Barbacoas, a lowland rainforest site in the Chocó biogeographic region of southwestern Colombia. This site was originally surveyed by AMNH personnel in 1912, providing a 109-year interval over which to examine morphological change. Among all resurveyed localities, Barbacoas stands out for having maintained exceptional forest continuity with >95% natural land cover at local (1 km), landscape (5 km), and regional (20 km) scales when considering changes in the human footprint index (Correa Ayram et al. 2020).

We analyzed morphological change over 109 years by comparing specimens from the original (1912) and the modern (2021) expeditions in Barbacoas, Colombia, to investigate long-term morphological trends in 23 species of lowland rainforest birds. We estimated both absolute changes in body size and traits, as well as relative changes in body shape. Given that Barbacoas has experienced minimal landscape transformation over the past century, this site offers a unique opportunity to isolate potential morphological responses driven primarily by climate change. Based on known adaptations of body size to enhance heat dissipation (Bergmann 1847; Gardner et al. 2011) and increases in the size of thermoregulatory appendages, such as bills and tarsi (Allen 1877; Greenberg et al. 2012; Tattersall et al. 2017), as well as previous studies on morphological responses of birds to climate change (Goodman et al. 2012; Gardner et al. 2019; Weeks et al. 2020; Jirinec et al. 2021), we hypothesize that if climate change is exerting a selective pressure on the physiology of forest birds, then we would expect to observe reductions in body size and increases in the relative size of appendages involved in heat dissipation linked to historical increases in temperature. By examining both absolute changes in body size and traits, as well as relative changes in body shape across 23 resident landbird species, this study provides unique insights into long-term morphological responses and potential adaptations to anthropogenic climate change.

Materials and methods

1912 vs. 2021 surveys

To examine morphological changes, we analyzed bird specimens collected during two intensive sampling periods at Barbacoas, separated by 109 years: the historical 1912 expedition and a 2021 resurvey. The century-old collection comprises 158 specimens gathered by W. B. Richardson between August 3 and September 10, 1912, for the American Museum of Natural History (AMNH, Chapman 1917). The modern collection consists of 265 specimens collected between October 8 and 19, 2021, by the Colombian Resurvey Project during the "Alas, Cantos y Colores" expeditions (Gómez et al. 2022). The 1912 specimens, collected using shotguns, are largely housed at the AMNH, whereas the 2021 specimens, obtained by mist nets, are housed at the National Bird Collection, Instituto de Ciencias Naturales (ICN), Universidad Nacional de Colombia. All specimens studied were prepared as round study skins. The differing collection methods may introduce sampling bias, as shotgun collectors could potentially be more selective (for larger size or external appearance) than the passive sampling of mist nets. However, Richardson lacked binoculars or other optical equipment, so his ability to selectively target specific individuals was likely limited. Moreover, the differences we are observing are on the order of millimeters, variation so subtle that it would have been imperceptible to collectors in the field. A more relevant bias from differing sampling methods is the underrepresentation in our comparisons of canopy-dwelling species for which Richardson collected series (e.g., *Querula purpurata*, Purple-throated Fruitcrow) but that were not captured in our mist net lines. Therefore, our inferences are restricted only to the subset of the local assemblage of species sampled in both time periods.

Study area

Barbacoas is located in southwestern Colombia (1.6625°, −78.1464°), in the department of Nariño (Fig. 1a), within the Pacific lowlands of the Chocó Biogeographic Region, which is a recognized biodiversity hotspot (Myers et al. 2000). The original collector, W. B. Richardson, sampled the lowlands around the town of Barbacoas, at approximately 70 m elevation. We did not include the nearby foothill locality (366 m) of Buenavista, which was also sampled by Richardson. Our 2021 resurvey focused on two sampling localities, Entre Ríos (1.6591°, −78.1475°), and Mingoya (1.6192°, −78.0722°), near the town of Barbacoas (Fig. 1b), in areas that have maintained their forest structure since the original 1912 expedition. The landscape remains largely forested, with approximately 99% tree cover, of which 74% (238 000 ha) corresponded to primary forest as of 2000 (Global Forest Watch 2025). The region is characterized by lowland rainforest with exceptionally high annual rainfall (4500 to 9254 mm per year) and a mean temperature of 26 °C (Guevara et al. 2016).

To estimate long-term trends in climate at the sampling sites, we used temperature and precipitation data extracted from the Climatic Research Unit (CRU) of the University of East Anglia (Harris et al. 2014) for the 0.5-degree cell encompassing both sampling sites.

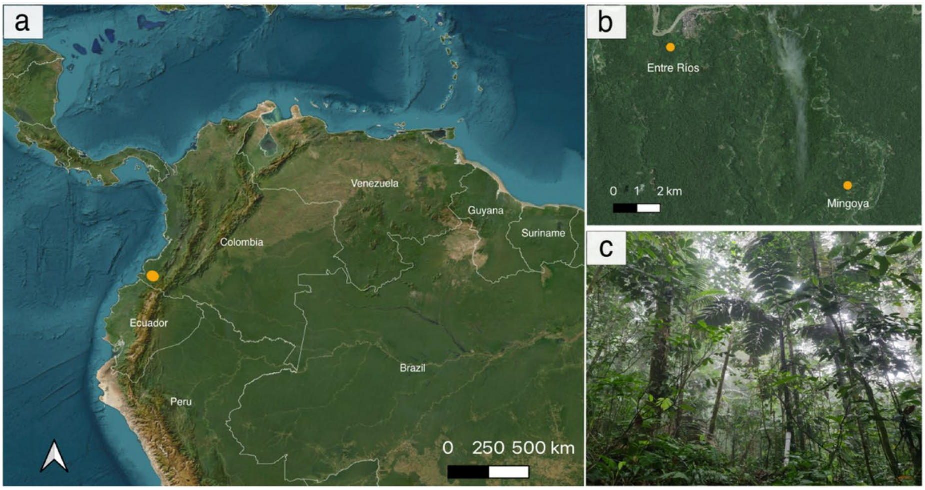

Fig. 1 Location of Barbacoas, Nariño, Southwestern Colombia (**a**), sampling sites (**b**), forest cover in the locality Mingoya (**c**)

We filtered the dataset to include only records from 1950 onward (when the number of weather stations available for interpolation increased sufficiently) and calculated annual mean temperature and total precipitation. Statistical significance was assessed through linear regression models, with year as the predictor variable and mean temperature or total precipitation as the response variables.

Data collection

From a total of 172 species collected in 1912 and 100 in 2021, 24 species had sufficient sampling (i.e., at least three specimens per survey period) for statistical comparisons. We excluded *Actitis macularius* (Spotted Sandpiper) from the dataset, which was unusual for being a migratory shorebird. We thus analyzed morphometric changes in 23 year-round resident landbirds (Table 1, S1, Fig. S4). The final dataset consisted of 423 individuals (158 from 1912, and 265 from 2021), with an average of seven historical and 11 modern specimens per species. Sample sizes ranged from 35 individuals for *Manacus manacus* (White-bearded Manakin) to 11 for *Saltator maximus* (Buff-throated Saltator) (Table S1, S2). All 2021 specimens were measured in 2024 after completing curatorial processing, including oven-drying (48–72 h), quarantine, and storage in collection cabinet drawers. Given that post-mortem shrinkage primarily occurs within the first few months after preparation and

Table 1 Twenty-three bird species from the Barbacoas rainforests included in this study, sampled in two time periods, 1912 and 2021. The dataset included four hummingbird species (Trochilidae), one puffbird (Bucconidae), and 18 passerine species from seven families (Supplementary Fig. S4). Subspecies identifications are based on curatorial work at ICN. English names and taxonomic sequence follow the South American Classification Committee (SACC, Remsen et al. 2025)

Family	Study taxon	English name	Sample size
Trochilidae	*Florisuga m. mellivora*	White-necked Jacobin	15
	Phaethornis striigularis subrufescens	Stripe-throated Hermit	15
	Androdon aequatorialis	Tooth-billed Hummingbird	15
	Polyerata rosenbergi	Blue-headed Sapphire	22
Bucconidae	*Malacoptila panamensis poliopis*	White-whiskered Puffbird	15
Thamnophilidae	*Thamnophilus a. atrinucha*	Black-crowned Antshrike	19
	Myrmotherula pacifica	Pacific Antwren	14
	Poliocrania exsul maculifer	Chestnut-backed Antbird	24
	Gymnopithys bicolor aequatorialis	Bicolored Antbird	20
	Hylophylax n. naevioides	Spotted Antbird	17
Furnariidae	*Glyphorynchus spirurus subrufescens*	Wedge-billed Woodcreeper	20
Pipridae	*Lepidothrix velutina minuscula*	Velvety Manakin	31
	Manacus manacus bangsi	White-bearded Manakin	35
Onychorhynchidae	*Myiobius barbatus aureatus*	Sulphur-rumped Flycatcher	15
Tyrannidae	*Mionectes olivaceus hederaceus*	Olive-striped Flycatcher	18
Troglodytidae	*Cantorchilus nigricapillus connectens*	Bay Wren	12
	Microbates c. cinereiventris	Tawny-faced Gnatwren	16
Thraupidae	*Tachyphonus delatrii*	White-shouldered Tanager	19
	Ramphocelus flammigerus icteronotus	Flame-rumped Tanager	19
	Sporophila corvina ophthalmica	Variable Seedeater	22
	Sporophila n. vivida	Yellow-bellied Seedeater	16
	Saltator maximus iungens	Buff-throated Saltator	11
	Stilpnia larvata fanny	Golden-hooded Tanager	12

then specimen size stabilizes (Knox 1980; Winker 1993; Kuczyński et al. 2002), measurements taken at this stage should be comparable to those of historical specimens from 1912.

For each specimen, we collected nine morphometric measurements: total bill length (from the base of the skull to the tip of the maxilla), bill length from nostrils (from the anterior edge of the nostril to the tip of the maxilla), bill depth (at the anterior edge of the nostrils), maxilla depth (at nostrils), bill width (at nostrils), tarsus length, Kipp's distance (KD; length from the tip of the first secondary to the longest primary remige), wing length (WL; wing chord), and tail length (Baldwin et al. 1931). We excluded wing and tail measurements from specimens with heavily worn or molting feathers. Tarsus, bill traits, and Kipp's distance values were taken with a digital caliper (iGaging IP54) with a precision of 0.01 mm, whereas wing and tail lengths were taken with a top ruler to the nearest 1 mm. We calculated the surface area of the maxilla from an adjustment in the estimation of the area of a cone: ((bill width + maxilla depth)/2)*total bill length*π (Ryding et al. 2025). We calculated the hand-wing index (HWI) as 100*(KD/WL) (Baldwin et al. 1931; Claramunt et al. 2012; Sheard et al. 2020).

To ensure measurement accuracy and assess measurement error, a single measurer (NPA) measured each trait three times per specimen. To evaluate the consistency of measurements within individuals, we calculated repeatability of the three measures by trait using an analysis of variance (ANOVA). From this analysis, we extracted the between-individual (BV) and within-individual (WV) variances and calculated repeatability (R = BV/(BV + WV) (Lessells and Boag 1987). Repeatability was greater than 0.89 for all traits (Table S3, values close to 1 indicate high consistency in measurements). We then calculated the mean from the three repeated measurements for each trait and individual. We found no outliers in our data (values > 4 SDs from the mean). To estimate the degree of variability per trait per species we estimated the coefficient of variation (%CV=(SD/Mean)*100), which expresses the unbiased sample standard deviation as a percentage of the sample mean per species (Welham et al. 2014). Bill depth was excluded from the analyses because many 1912 specimens (78%) had open bills, and so we used maxilla depth (see above) as a proxy of bill depth. Our final trait dataset contained eight measurements.

Because we had no data on the body mass of the 1912 Barbacoas specimens, we used a principal component analysis (PCA) to devise an index of body size. Specifically, we performed a PCA on the mean trait values for all traits of all individuals across species, extracting PC1 as a proxy for body size (Pigot et al. 2020). Because of the size and shape disjunction of Trochilidae (hummingbirds) in relation to all other birds, and because we were not able to measure their tarsi, we performed a separate PCA for hummingbirds. For non-hummingbird species, we excluded HWI from the PCA because it did not increase proportionally with body size and because 13 out of 19 species showed moderate variation (e.g., CV between 10% and 30%, Table S4). We first performed a Bayesian PCA to impute missing data (e.g., for broken tarsi or bills, molting wings or tails) for hummingbirds and non-hummingbirds independently; for this, we used the *bpca* method of the 'pcaMethods' R package (Stacklies et al. 2007) with two components for re-estimation (nPCs = 2). Then we performed a PCA with the *prcomp* function of the 'stats' R package (R Core Team 2024), after logarithmic transformation of the mean trait values. PC1 explained 73% of the variation in hummingbirds (Table S5) and 72% of the variation in non-hummingbirds (Table S6). For both PCAs, PC1 was initially negatively loaded for all traits, meaning that all traits were negatively correlated with PC1 (Tables S5, S6). However, we wanted PC1 to be positively correlated with traits such that higher PC1 values indicated larger body size. We therefore performed a mirror transformation of PC1 i.e., multiplying all PC1 values by −1 (Tables S5, S6). This transformation preserves the geometry of the PCA while rendering PC1 values more intuitive (Figs. S1, S2). Finally, to generate our body size index, we subtracted from each PC1 score the minimum PC1 value and added 1, so that all index values were positive.

Nine of the species are not sexually dimorphic and so their 1912 specimens could not be sexed without further information (i.e., annotated tags). We therefore did not have sufficient sample sizes to assess variation between sexes; for each species, males and females were grouped together for all analyses. Similarly, although our dataset consisted of mostly adult individuals, and we excluded fledglings and juveniles, precise age data are not available from 1912 specimens (i.e. skull pneumatization); we also grouped all age classes together in the analysis.

Analysis

To assess whether bird populations of 23 landbirds have changed morphologically in Barbacoas, we conducted Bayesian hierarchical models within a mixed effects framework. We first standardized the mean trait values of each species by calculating the Z-scores at the species level (Z = Trait value-Trait mean/Trait SD). All species were included in the same model, accounting for species as random effects via species-specific intercepts (alphas), species-specific changes in traits over time (deltas), as well as a species-specific error structure. This approach allows both inference on overall effects of change (via hyper-parameters) and on individual species effects (Neate-Clegg et al. 2024b). We ran the models using the JAGS Bayesian graphical modeling program (Plummer 2003) via the R package 'R2jags' (Su and Yajima 2024) using R ver. 4.4.0 (R Core Team 2024).

We estimated morphological changes using two approaches, the first by analyzing changes in absolute body and trait size between historical and modern specimens, and the second by analyzing changes in relative body shape by employing ratios of morphological measurements. For the latter, we calculated ratios by taking the log-transformed values of each trait (as allometric correction) and dividing it by its body size index.

We ran Bayesian analyses where all priors were vague (e.g. normal (0, 100), or gamma (0.001, 0.001) for zero-bound parameters). The models included three chains that ran for 50,000 iterations including a burn-in of 10,000, followed by a 40-fold thinning applied to the remaining posteriors. To evaluate the convergence of Bayesian models, we calculated the Potential Scale Reduction Factor (PSRF) where values close to 1 indicate convergence and values much higher than 1 indicate no convergence (Gelman and Rubin 1992). All Bayesian models presented PSRF < 1.05 indicating that the MCMC chains converged (Table S2). We extracted the mean as well as the 2.5 and 97.5% quantiles (representing the 95% credible intervals) for each parameter. We also calculated the percentage of posteriors above or below 0 as a measure of the strength of evidence.

Because aspects of morphology are linked to phylogenetic relatedness among species, it was important to test for phylogenetic nonindependence in a sensitivity analysis. For our species set, we extracted 1000 phylogenetic trees with the Hackett backbone from birdtree.org (Jetz et al. 2012). We then created a consensus tree using the function *ls.consensus* from the package 'phytools' (Revell 2012). From this tree we calculated the phylogenetic covariance matrix across species. We then directly incorporated this matrix into a model that was otherwise similar in structure to our main models, but allowing for phylogenetic similarity in the trait means as well as the trait deltas. To quantify phylogenetic signals, these models directly estimated Pagel's lambda for the trait intercepts and deltas (Pagel 1999). We found very little phylogenetic signal in the model, with lambda values below 0.02 for all trait intercepts, and lambda values around 0.1 for trait deltas (Table S3).

Results

Temperature and precipitation trends

The linear model results revealed a significant increase in annual mean temperature from 1950 to 2025, with an estimated rate of 0.118 °C per decade (β =0.0118, $p < 0.001$, $R^2 = 0.317$) representing a total increase of approximately 0.88 °C in the last 75 years (Fig. S5). In contrast, annual total precipitation did not show a significant trend (β = −2.91, $p = 0.179$, $R^2 = 0.025$). However, the estimated rate of change of −2.91 mm per year suggests a cumulative reduction of 218.25 mm over the same period (Fig. S6), although this decrease was not statistically significant.

Changes in body and trait size

For hummingbirds there was weak evidence that body size index was lower in recent specimens (coefficient = −0.19, 95% Bayesian CrI = −1.06 to 0.67; Pr(coefficient <0) =69%), with strong evidence (i.e., 95% CrI did not overlap 0) of a decrease in body size for one species (*Florisuga mellivora*; Figs. 1d and 2a, and S4). In non-hummingbirds, there was moderate evidence that body size index showed an average increase in recent specimens (coefficient =0.11, 95% CrI = −0.07 to 0.31; Pr(coefficient >0) =88%), with strong evidence of increases in body size for three species and decreases for one (Fig. 2b).

Hummingbirds showed larger HWI values in recent specimens (coefficient =1.00, 95% CrI = −0.01 to 2.05; Pr(coefficient >0) =97%), with strong evidence for three of the four species (Fig. 2a). Tarsus length did not change overall (Table 2) but we found strong evidence of an increase for one of the 19 non-hummingbird species: *Malacoptila panamensis* (White-whiskered Puffbird; Fig. S1 and S4). Total bill length, bill length from nostrils, and bill width did not differ between sampling periods (Table 2, Fig. S3). In contrast, maxilla depth increased overall (coefficient =0.53, 95% CrI =0.23 to 0.83; Pr(coefficient >0) =100%) with strong evidence of increases for ten out of the 23 species (Fig. 2c). Maxilla area increased overall (coefficient =0.32, 95% CrI =0.03 to 0.62; Pr(coefficient >0) =100%), with strong evidence of an increase for one species (Fig. S3b). For recent specimens, on average, wing length showed a decrease (coefficient = −0.42, 95% CrI = −0.71 to −0.12; Pr(coefficient <0) =99%) with strong evidence of a decrease for four species. Tail length increased between the original and modern expeditions (coefficient =0.74, 95% CrI =0.43 to 1.05; Pr(coefficient >0) = 100%), with strong evidence of increases for 14 species (Fig. 2c).

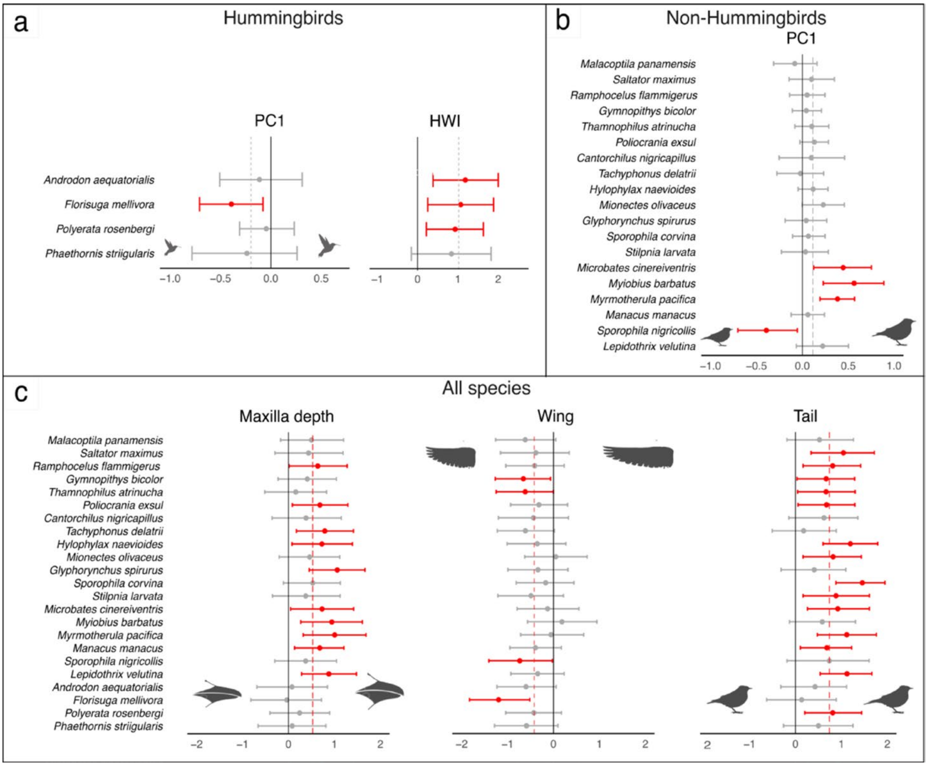

Fig. 2 Temporal changes in trait size between historical and modern bird specimens collected in Barbacoas, Colombia. Differences in absolute trait size are shown for hummingbirds (**a**), non-hummingbirds (**b**), and all species (**c**). Points represent mean values, and bars represent the 95% Bayesian credible intervals. Points and bars are red when not overlapping 0. The dotted line shows the group mean (i.e. model hyper-parameter); it is red when the interval does not include 0 and gray when it does. Species are arranged by body size based on PC1 loadings

Changes in body proportion

Overall, morphological ratios (i.e., trait measurements in relation to body size index) did not differ between historical and contemporary hummingbird specimens for total bill length, bill length from nostrils, maxilla area, wing, HWI, and tail, except for one species, *Florisuga mellivora* (White-necked Jacobin; Table 2; Fig. 3a). In that species, the five traits showed strong evidence of proportionally greater increases in size over time. In non-hummingbirds, the relative size of the seven traits did not change overall (Fig. 3b), but the relative total bill length (coefficient = −0.03, 95% CI = −0.18 to 0.13; Pr(coefficient < 0) = 64%) showed strong evidence of decreases for recent populations of four species, and relative bill length from the nostrils (coefficient = −0.02, 95% CrI = −0.18 to 0.13; Pr(coefficient < 0) = 58%) was smaller for four species, and larger in one.

Relative maxilla depth did not change overall but showed strong evidence of decline in two species, and increased in three (Fig. 3b). Relative bill width and maxilla area did not change between surveys, but decreased for three species and increased for one. Relative wing length exhibited minimal change, but we found strong evidence of decrease in four

Table 2 Results of the hierarchical bayesian models comparing absolute and relative morphological traits in hummingbirds and non-hummingbirds for 1912 and 2021 bird specimens, showing the estimated coefficients, 95% credible intervals (CrI), and posterior probabilities (Pr(coefficient)). For details on the specimens included in this study see Table S1

	Coefficient	95% CrI	Pr (coefficient)
Absolute trait			
Hummingbird PC1	−0.19	−1.06, 0.67	< 0 = 69%
Non-Hummingbirds PC1	0.11	−0.07, 0.31	> 0 = 88%
HWI (hummingbirds)	1.00	−0.01, 2.05	> 0 = 97%
Total bill length	0.23	−0.07, 0.55	< 0 = 6%
Bill length from nostrils	0.23	−0.07, 0.53	< 0 = 6%
Maxilla depth	0.53	0.23, 0.83	> 0 = 100%
Bill width	0.07	−0.22, 0.37	< 0 = 32%
Maxilla area	0.32	0.03, 0.62	> 0 = 100%
Tarsus (non-hummingbirds)	0.02	−0.32, 0.37	< 0 = 46%
Wing length	−0.42	−0.71, −0.12	< 0 = 99%
Tail length	0.74	0.43, 1.05	> 0 = 100%
Relative traits in hummingbirds			
Total bill length	0.09	−0.79, 1.02	< 0 = 41%
Bill length from nostrils	0.07	−0.78, 0.94	< 0 = 42%
Maxilla depth	−0.01	−0.81, 0.82	< 0 = 51%
Bill width	0.01	−0.84, 0.81	< 0 = 47%
Maxilla area	−0.04	−0.20, 0.12	< 0 = 69%
Wing length	0.13	−0.76, 1.01	< 0 = 37%
Tail length	0.08	−0.82, 0.93	< 0 = 41%
HWI	0.19	−0.71, 1.15	< 0 = 29%
Relative traits non-Hummingbirds			
Total bill length	−0.03	−0.18, 0.13	< 0 = 64%
Bill length from nostrils	−0.02	−0.18, 0.13	< 0 = 58%
Maxilla depth	0.002	−0.14, 0.15	< 0 = 49%
Bill width	−0.01	−0.16, 0.14	< 0 = 56%
Maxilla area	0.15	−0.69, 1.04	< 0 = 34%
Tarsus	−0.02	−0.18, 0.13	< 0 = 64%
Wing length	−0.02	−0.17, 0.14	< 0 = 60%
Tail length	−0.02	−0.18, 0.13	< 0 = 64%

species and increased in one. Relative tail length decreased in three species, and relative tarsus length showed little change, despite a strong decrease in four species and an increase in one (Table 2). Notably, the species showing strong evidence of trait changes are mostly among the smaller-bodied taxa.

Discussion

Our study, spanning more than a century of morphological change in Barbacoas, a lowland tropical rainforest bird community in Colombia, reveals a complex mosaic of responses that represent a challenge to simple interpretations of climate-driven changes. Resident landbirds in Barbacoas have experienced several morphological shifts since 1912, with contrasting patterns between taxa: while hummingbirds showed consistent body size decreases,

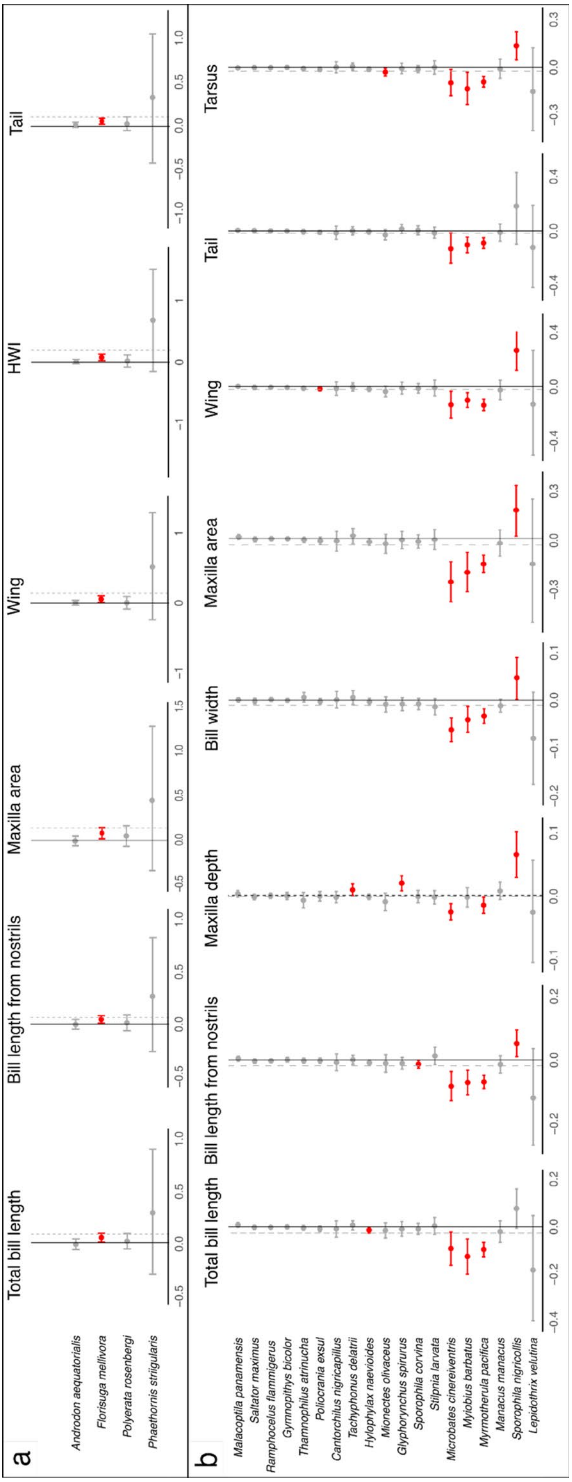

Fig. 3 Temporal changes in trait size in relation to index of body size (PC1) between historical and modern bird specimens collected in Colombia for hummingbirds (**a**) and non-hummingbirds (**b**). Points represent mean values, and bars represent the 95% Bayesian credible intervals. Points and bars are red when not overlapping 0. The dotted gray line shows the group mean (i.e. model hyper-parameter). Species are arranged by body size based on PC1 loadings

most non-hummingbirds exhibited size increases, with strong evidence for three species. Beyond these divergent body size trends, we documented consistent changes in appendage dimensions across species, including increased maxilla depth in nearly half the species and widespread shifts in wing-tail proportions. These diverse responses, occurring in a rainforest landscape that has maintained exceptional habitat continuity, may reflect factors beyond direct thermal stress. In the region, the mean annual temperature has increased approximately 0.88 °C in the last 75 years. This change is comparable to the 0.58 °C increase in Tanzania over the last three decades (Neate-Clegg et al. 2024b) and the 1.00 °C and 1.65 °C increases observed in the wet and dry seasons, respectively, over the past 40 years in Manaus (Jirinec et al. 2021). Our findings from Barbacoas highlight the importance of studying long-term morphological changes to better understand how bird communities respond to anthropogenic climate change particularly in well-preserved tropical landscapes.

Our results show mixed trends in body size, with decreases over time in *F. mellivora* and *Sporophila nigricollis* (Yellow-bellied Seedeater; average reduction of 1.9%), and increases in three non-hummingbird species: *Microbates cinereiventris* (Tawny-faced Gnatwren), *Myiobius barbatus* (Sulphur-rumped Flycatcher), and *Myrmotherula pacifica* (Pacific Antwren; average increase 3%; Fig. 1d). Decreased body size, observed through both mass measurements and PCA analysis of multiple morphological traits over time has been widely reported as a potential response to climate warming in regions such as the UK (Yom-Tov et al. 2006), Israel (Dubiner and Meiri 2022), North America (Van Buskirk et al. 2010; Weeks et al. 2020; Youngflesh et al. 2022), and the Amazon (Jirinec et al. 2021). Notably, the only other similar study on Neotropical birds (Jirinec et al. 2021) reported a decrease in body mass for 77 lowland species (significant for 36, with a reduction up to 1.8% per decade) in the Brazilian Amazon across 40 years. These patterns align with the heat exchange hypothesis (smaller bodies are more efficient at dissipating heat, Brown and Lee 1969), offering an adaptive advantage in warmer climates. However, contrasting findings of increased body size suggest that a decrease in body size is not a universal response to climate change (Teplitsky and Millien 2014; Gardner et al. 2019).

Increased body size has been reported in studies for birds along California's Central Coast (Goodman et al. 2012) as well as the Usambara Mountains of Tanzania (Neate-Clegg et al. 2024b). In our study there was weak evidence of body size increases across non-hummingbirds, with three species showing strong evidence of increasing body size: *M. cinereiventris* (Tawny-faced Gnatwren), *M. barbatus* (Sulphur-rumped Flycatcher), and *M. pacifica* (Pacific Antwren). Possible explanations include the starvation resistance hypothesis, which suggests that larger-bodied individuals are better at surviving in unpredictable environments due to their greater capacity to store body reserves (Kooijman 1986; Cushman et al. 1993), and the population size influence which links decreased population size to larger territories and greater access to resources, resulting in larger body size (Neate-Clegg et al. 2024). Likewise, changes in temperature and precipitation from climate change could affect primary productivity, food availability and the ability of birds to forage, thereby influencing body size (Yom-Tov and Geffen 2011; Goodman et al. 2012; Boyle et al. 2020). Further research, incorporating ecological and demographic data is needed to understand the factors driving these contrasting trends in body size.

Additionally, habitat preferences may also play a role in the variation in observed trends of morphological change across species (Jirinec et al. 2021). Species showing decreases in body size, such as *F. mellivora* and *S. nigricollis* are associated with open habitats and edges

(Stiles et al. 2020; Rising et al. 2020), potentially exposing them to higher temperatures. In contrast, understory species like *M. cinereiventris* and *M. barbatus* (Atwood et al. 2020; Schafer 2024), or forest edge species like *M. pacifica* (Zimmer and Isler 2020) may experience lower temperatures due to the buffering provided by the canopy.

One notable finding in our study is the observed trend of increasing absolute tail size over a century, with strong evidence of longer tails in 60.8% of the species analyzed (14 out of 23, average growth of 4.4%). The change in tail length appears to be proportional to increasing body size in most species, as indicated by a lack of change in relative tail length (Fig. 2b). We are unaware of any studies specifically evaluating changes in tail length over time. It has been reported that forest birds tend to have shorter wings compared to those in open habitats. This influences tail length, which is generally longer in forest birds, to compensate for reduced lift due to shorter wings (Balmford et al. 1993; Thomas and Balmford 1995). In our study, we observed a slight overall decrease in wing length accompanied by a pronounced increase in tail length. This pattern could be linked to changes in forest structure across time, resulting in forests increasingly dominated by denser secondary vegetation due to successional dynamics triggered by the loss of sensitive species (Svenning and Sandel 2013). In this context, tail elongation could serve as an adaptation to compensate for shorter wings, improving maneuverability in dense habitats (Balmford et al. 1993; Thomas and Balmford 1995). While these explanations focus on functional adaptations related to flight performance (natural selection), sexual selection may also contribute to the observed tail elongation. In many bird species, females often favor longer tails in mate choice (Balmford et al. 1993; Aparicio et al. 2003). Investigating whether the species showing the most pronounced changes in tail length also use their tails in mating displays could help clarify the extent to which sexual selection influences these patterns.

Our analysis revealed strong evidence that increases in maxilla depth (a proxy for bill depth) have occurred in 43.5% (10 out of 23) of the species analyzed. We also found a general trend toward an increase in maxilla area, but this change only showed strong evidence in one species. The absence of strong evidence of changes in maxilla area suggests that detecting shifts may be challenging, particularly in smaller birds, due to the maxilla's small surface area or measurement noise from estimation calculations. Nevertheless, the observed increases in bill size are consistent with Allen's rule, which predicts that animals in colder climates tend to have shorter body appendages than those in warmer regions, where larger appendages facilitate heat dissipation (Allen 1877; Greenberg et al. 2012; Tattersall et al. 2017; Tian and Benton 2020). Consequently, rising global temperatures are expected to drive increases in traits such as tarsus length (we found strong evidence of tarsus length change in only one species) and bill size (Gardner et al. 2014; Campbell-Tennant et al. 2015). Indeed, an increase in bill area over more than a century has been reported in Australian birds, potentially as a response to mitigate the thermal stress caused by climatic warming (Campbell-Tennant et al. 2015; Ryding et al. 2024a). The greater response in bill size compared to tarsus dimensions aligns with findings that birds can more tightly regulate blood flow to tarsi than to bills, making bills more susceptible to temperature-driven changes (McQueen et al. 2023). This pattern mirrors more consistent temporal increases in bill surface area than in tarsus observed in temperate-zone birds (Krugler et al. 2025). However, beyond thermoregulation, climate change may also indirectly influence bill size through its effects on temperature and precipitation patterns, which alter primary productivity (Campbell-Tennant et al. 2015), thereby affecting food availability or foraging habitats, and potentially selecting for larger bills (Grant and Grant 2002).

We found a strong decrease in wing length in four of the 23 species, contrasting with broader trends from other regions, which report both increases and decreases. Temporal studies in Australia (50 years, Gardner et al. 2019; 104 years, Ryding et al. 2024a), Europe (120 years, Salewski et al. 2014), and the United States (45 years, Van Buskirk et al. 2010) link wing length decreases to climate-driven temperature changes, using wing length as a proxy for decreasing body size. These contrast with the increase in wing length over time in both resident (27–50 years, Goodman et al. 2012; 29 years, Youngflesh et al. 2022) and migratory birds (40 years, Weeks et al. 2020) in the United States, and tropical regions (36 years, Neate-Clegg et al. 2024b; 40 years, Jirinec et al. 2021). Longer, pointier wings in resident birds are sometimes linked to fragmented landscapes requiring greater dispersal (Bowlin and Wikelski 2008; Desrochers 2010; Hermes et al. 2016). The study on Neotropical lowlands birds by Jirinec et al. (2021) was conducted in a conserved area where forest cover has increased over time (Rutt et al. 2019). In contrast, our results, from a conserved area, suggest that decreases in wing length may relate to subtle changes in forest structure rather than fragmentation. However, we also found more pointed wings in three of the four hummingbird species. These contrasting results highlight the need to study how forest composition in conserved Neotropical areas influences morphological adaptations (Jirinec et al. 2021).

Our results on morphological ratios suggest that species of smaller body size may be undergoing more rapid morphological changes compared to larger species. This pattern is consistent with previous findings indicating that smaller species may respond more rapidly to environmental changes (Zimova et al. 2023; Neate-Clegg et al. 2024b). Among the species analyzed, the hummingbird *F. mellivora* exhibits the most distinct patterns, with increases in bill length, wing length, HWI, and tail length that are proportionally greater than its increase in body size. This combination of changes suggests potential morphological adaptations to environmental shifts or alterations in foraging patterns. Such pronounced changes across multiple traits may reflect the interplay of selective pressures acting simultaneously on flight efficiency, thermoregulation, resource acquisition, and sexual selection. After approximately 110 years this forested region has experienced clear evidence of climate change. Over the past 75 years, temperature has increased by 0.88 °C, and annual precipitation has decreased by 218 mm. From 1982 to 2011 the amplitude of the annual precipitation cycle also increased, indicating a greater contrast between wet and dry seasons (IDEAM-UNAL 2018). Moreover, the last 40 years have seen more extreme precipitation events (dos Santos et al. 2024; Gallego et al. 2019). Under this climatic context, birds are exhibiting morphological changes in complex ways that challenge established theories and empirical evidence—specifically, smaller body sizes paired with larger appendages such as wings and tarsi (Bergmann 1847; Allen 1877; Gardner et al. 2011; Tian and Benton 2020). These unexpected patterns call for further investigation into how climate change may be driving cascading effects across multiple ecological dimensions, including community structure (Le Roux and McGeoch 2008; Alarcón and Pabón 2013; Svenning and Sandel 2013), species interactions (Gibert and DeLong 2014), resource availability and predictability (phenology) (Yom-Tov and Geffen 2011; Piao et al. 2019), and habitat structure (Auer and Martin 2013), rather than directly impacting birds' physiology. The variability in species-specific morphological responses may be attributed to climate change impacts that are not yet strong enough to drive consistent shifts across the entire community, with idiosyncratic factors potentially shaping each species' response. This complexity highlights the need to explore non-linear models of climate-driven morphological change, where warming temperatures indirectly influence birds through ecological shifts. Although reductions in body size could theoretically facilitate heat dissipation, the magnitude of these changes is often too small to confer meaningful physiological advantages, and their adaptive significance remains uncertain (Nord et al. 2024). These findings emphasize the variability of responses within bird communities to long-term environmental changes and underscore the importance of considering indirect pathways to better understand the link between climate change and avian morphology.

The century-long morphological changes we documented in a near-pristine Colombian forest demonstrate complex and species-specific responses to environmental changes. Our findings suggest that multiple mechanisms shape avian morphology over extended time periods in the face of global change. The contrasting patterns we observed, from divergent size trends between hummingbirds and other birds, to consistent changes in beak size and wing/tail proportions, highlight the need for further research to disentangle the roles of climate change, habitat alteration, and ecological interactions in shaping avian morphology in the Anthropocene. In evaluating these patterns, we note that neither post-mortem shrinkage, which stabilizes within months after preparation (Winker 1993; Wilson and McCracken 2008), nor differences in collecting methods (shotguns in 1912 versus mist nets in 2021) can account for the magnitude of the observed morphological changes. Importantly, focus needs to shift to the mechanisms driving adaptation or phenotypic plasticity linked to climate change, and the interplay between physiological responses, species interactions, and species' relationships to their environment. Integrating long-term monitoring, behavioral and ecological data, experimental approaches, and continued museum specimen analyses will be key to identifying the drivers to these changes and predicting how bird communities may respond to future environmental change.

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Author contributions NPA drafted the first version of the manuscript with the contribution of AMC. NPA, CDC, JSP and AMC participated in the 2021 expedition. NPA examined and measured all specimens. MHCNC conceived the statistical design. NPA conducted the statistical analyses with support from MHCNC. CDC, AMC, and NOP conceptualized and administered the Colombian Resurvey Project. All authors contributed to the editing and revisions.

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Data availability Specimens included in this study are available at AMNH, MCZ, USNM, FMNH, and ICN (Supplementary Material Table S1).

Code availability Not applicable.

Declarations

Competing interests The authors declare no competing interests.

Ethical approval Research was conducted under Colombian law (Decrees 1375 and 1376, 2013, Ministry of Environment), with specimens deposited at the ICN National Bird Collection (national registry 005) and field activities authorized and accompanied by local communities.

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