


Variation in avian morphology along a short tropical elevational gradient

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Funding information

Third Millennium Alliance; Field Museum; University of Chicago

Associate Editor: Jennifer Powers

Handling Editor: Donald Franklin

Abstract

Patterns across species of intraspecific phenotypic variation with environment can shed light on the underlying drivers of adaptive evolution. Phenotypic variation within a species along tropical elevational gradients is of particular interest because species with narrow elevational ranges may still experience considerably varied environmental conditions. Here, we examine morphological variation in 27 tropical bird species, spanning 11 families and 3 orders, across a 675m elevational gradient in Western Ecuador. We analyzed a data set of six morphological variables in 3263 individual birds using multivariate analyses of variance (MANOVAs) and canonical correlation analyses (CCAs). We found that morphology varies significantly with elevation in 8 species, and that spatial segregation by age or sex was apparently not responsible for this result. The phenotypic traits that varied with elevation varied strongly by species. To the best of our knowledge, morphological variation over equally short elevational and horizontal distances across a diverse suite of vertebrate species has not previously been demonstrated.

Abstract in Spanish is available with online material.

KEYWORDS

altitudinal variation, ecological differentiation, elevational gradient, elevational variation, local adaptation, morphological variation

1 | INTRODUCTION

Geographical patterns of phenotypic variation can be useful for understanding underlying patterns of adaptive evolution and, therefore, for understanding the process of ecological speciation (Arnold, 1983; Mayr, 1963; Van Valen, 1965). Within a species, variation between populations may be driven by adaptive evolution under different selection regimes in regions with different environmental conditions (Mullen et al., 2009; Pitchers et al., 2013; Rundle & Nosil, 2005; Schluter, 2009). A correlation between phenotype and environment across populations or sub-populations can therefore

provide evidence of local adaptation (Blanquart et al., 2012; Conover et al., 2009; Savolainen et al., 2013).

Tropical elevational gradients are excellent systems to explore patterns of adaptive divergence, as environmental conditions along with them can differ considerably over short spatial distances (Forero-Medina et al., 2011; Freeman & Freeman, 2014), and a relative lack of seasonal climatic variation may select for specialization to highly specific conditions (Janzen, 1967; Stevens, 1989). Average ambient temperatures are tightly correlated with elevation, approaching the adiabatic lapse rate, and may drop by 6.5° C with a one-kilometer increase in elevation (Córdova et al., 2016).

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Precipitation may also vary dramatically with elevation on tropical mountains, although the relationship is often not monotonic (Celleri et al., 2007; Sarmiento, 1986). Precipitation variability within the range of a species can have substantial fitness impacts, including in endotherms (Boyle et al., 2020). The structure and composition of forests change rapidly with bioclimatic conditions, and thus with elevation (Grubb et al., 1963; Grubb & Whitmore, 1966; Vazquez-Garcia & Givnish, 1998). Forest-dwelling species on elevational gradients in the tropics may thus experience considerable variation in habitat across their elevational ranges that may be correlated with considerable variation in selection pressure (Janzen, 1967; Stevens, 1989). Tropical mountains are often hotspots of biodiversity (Myers et al., 2000; Rahbek et al., 2019): selection pressures on elevational gradients in the tropics may be directly responsible for generating this biodiversity and are thus particularly interesting in this context. At the same time, the relatively small horizontal extent of tropical elevational gradients implies the existence of substantial gene flow. The effect of gene flow on adaptive divergence is a matter of debate (Lenormand, 2002; Sexton et al., 2014); however, gene flow may be expected to minimize the effects of genetic drift and isolation by distance, which may otherwise hamper the interpretation of phenotype-environment correlations (Sexton et al., 2014).

Among birds, there is substantial evidence that natural selection can drive phenotypic divergence along tropical elevational gradients (Bertrand et al., 2016; Bulgarella et al., 2007; Chaves et al., 2007; Cheviron & Brumfield, 2009; Gutiérrez-Pinto et al., 2014; Milá et al., 2009; VanderWerf, 2012). Biogeographical “rules” based on the physiological costs of thermoregulation, such as Bergmann’s rule, which predicts an increase in body-size with temperature (Bergmann, 1847; James, 1983; Mayr, 1963), and Allen’s rule, which predicts a decline in appendage size with temperature (Allen, 1877), have sometimes been used to frame studies of adaptive evolution

along elevational gradients (e.g. Blackburn & Ruggiero, 2001; Brehm & Fiedler, 2004; Bulgarella et al., 2007; Freeman, 2017; Gutiérrez-Pinto et al., 2014; VanderWerf, 2012; Zamora-Camacho et al., 2014). Morphological variation along an elevational gradient has also been examined in the context of changing habitat structure (McCormack & Smith, 2008; Milá et al., 2009; Price, 1991). Across these studies, no consistent pattern of morphological variation with elevation is seen, indicating considerable variation along tropical elevational gradients in one or more of the following: the intensity of selection pressure, the rate of change in selection pressure, and compensatory mechanisms such as phenotypic or behavioral plasticity. Our understanding of the drivers of selection along elevational gradients is hindered by the absence of both comparative multi-taxon studies and negative results (but see Freeman, 2017).

Furthermore, studies of phenotypic divergence over elevational gradients in birds have frequently examined species with large elevational ranges spanning discrete habitats from moist forests in tropical lowlands to páramo ecosystems in sub-tropical or alpine highlands (e.g., Bertrand et al., 2016; Cheviron & Brumfield, 2009; Gadek et al., 2018; VanderWerf, 2012). Several species in which elevational divergence has been examined are habitat generalists (e.g. Cheviron & Brumfield, 2009; Gadek et al., 2018). Such broad elevational ranges are not typical of tropical avifauna (McCain, 2009; Stotz et al., 1996), and forest interior taxa in particular often have narrow ranges (Jankowski et al., 2013). Whether forest interior species also exhibit phenotypic divergence along elevational gradients, and if this divergence is detectable at small scales, remain open questions.

Here, we examine the relationship between morphology and elevation in 27 bird species along an elevational gradient in the coastal cordillera of western Ecuador. Though the coastal cordillera is considerably lower than the nearby Andes, it nonetheless

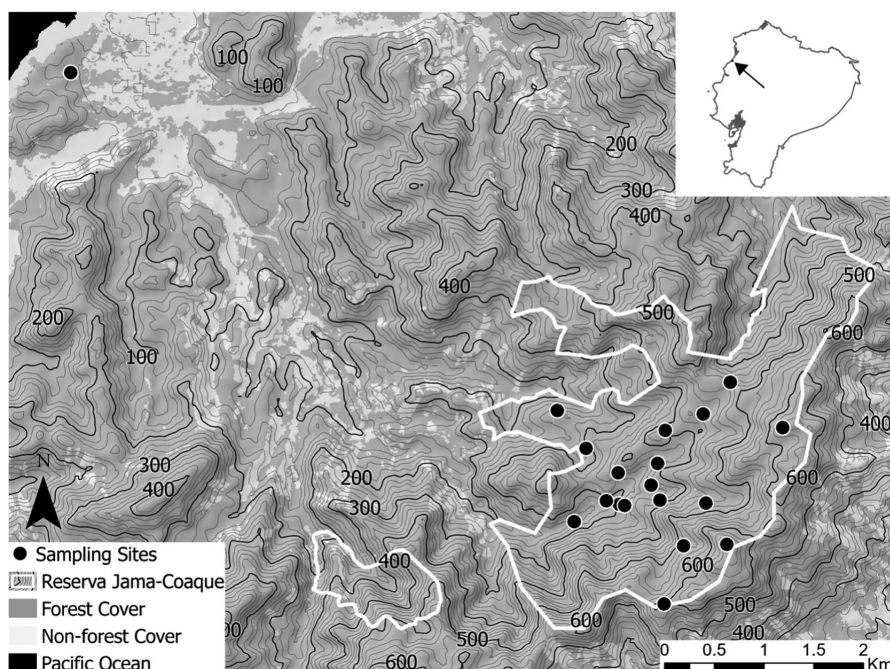


FIGURE 1 Map of study region. Contour lines show elevation in meters above sea level

encompasses substantial variation in habitat and microclimate. This is partially the result of fog-capture allowing cloud forest to exist on its peaks at an elevation (c. 500 m above sea level) much lower than is typical further inland (Becker et al., 2007; Becker & López-Lanús, 1997; Grubb, 1971). The 700-m elevational gradient thus gives rise to a continuum of interconnected forest types, from deciduous to humid to cloud forest, across just 8 horizontal kilometers. We aim to test whether this variation in forest habitat has led to an associated variation in morphology, presumably as a result of varying selection pressure. We do not make any assumptions about the specific drivers of variable selection and therefore have no a priori expectations about which traits are most likely to vary or whether any relationship with elevation is positive or negative. Rather, we aim to test whether morphological variation along a gradient can be detected at a small spatial scale and in a wide variety of species.

2 | METHODS

We collected morphological measurements at 21 sites spanning a 675-m elevational gradient in and around Reserva Jama-Coaque in Western Ecuador (0° 6' 57.75" S, 80° 7' 28.20" W) (Figure 1). This 6.5-km² ecological reserve consists largely of intact primary and mature secondary habitat. Sampling was conducted over two years (2018–19) with a hiatus in the rainy season; each site was sampled on up to two occasions in a given year and up to 3 days on a given occasion. Sites were generally in the forest interior or in immediately adjacent regenerating forest. One site was located outside Reserva Jama-Coaque in a dry forest approximately 8-km distant (Costa Jama; hereafter CJA). Mist nets were set up for up to five hours each day, beginning at dawn, except in rainy weather. Nets were checked every 30–40 minutes: captured birds were measured, weighed, and released. We collected six morphological measurements from each individual: unflattened wing chord (WC), length of longest rectrix (TL), bill length from nares to tip (BL), bill width at nares (BW), bill depth at nares (BD), and weight (W), as described in Pyle (1997). WC and TL were measured to the nearest millimeter; W was measured to the nearest 0.1 g with a digital scale; all other measurements were taken to the nearest 0.1 mm with vernier calipers. Morphological measurements were either taken by trainees and checked by experienced, certified banders, or were taken by the banders themselves. Data on molt and sexual characteristics (cloacal protuberance and brood patch) were also gathered when available. Site elevation was recorded with a Garmin eTREX Legend HCx GPS unit.

The resulting dataset included 5202 individuals from 178 species. We restricted our analyses to species with more than 50 captures and to species with a minimum of 400 m between lowest and highest captures. The data presented here thus include 3263 individuals from 27 species, with *N* ranging from 342 (ochre-bellied flycatcher, *Mionectes oleagineus*) to 49 (white-tipped sicklebill, *Eutoxeres aquila*). The 27 species include seven hummingbirds (Apodiformes: Trochilidae), 19 passerines from ten families, and

the white-whiskered puffbird (*Malacoptila panamensis*, Piciformes: Bucconidae) (Table 1). All 27 species are sedentary residents, and prefer forest interiors, forest edges, or secondary growth (Freile & Restall, 2018). Sampling locations for 4 species spanned a horizontal distance of 8 km, and for the remaining 23 species, just 2.5 km.

We used two methods to explore the relationship between morphology and elevation: Multivariate analyses of variance (MANOVAs) with elevation as a continuous independent variable, and canonical correlation analyses (CCAs). A MANOVA allows the exploration of the correlations between a set of dependent variables and the independent variable while accounting for the covariance between dependent variables. A CCA finds a linear combination of dependent variables that maximizes the correlation with a linear combination of independent variables, or in this case, a single independent variable (Härdle & Simar, 2007). The combination of methods was used to ensure the results were robust. In keeping with standard practice, we followed the MANOVAs with linear regressions for each dependent variable to identify the contributions of the dependent variables to any overall relationship between the dependent and independent variables (Stevens, 2012). The statistical significance of the CCAs was determined using permutation tests with 10,000 replicates. There is no clear consensus on the appropriate adjustment to *p*-values where the significance of multiple related tests are involved (Pike, 2011), as is the case here; we therefore implemented both a Bonferroni correction and a Benjamini–Hochberg false-discovery-rate correction, and evaluated the significance of our results under both approaches. We conducted analyses separately on all species after removing outliers, defined as measurements more than three standard deviations away from the mean for that species. We conducted analyses on raw morphological data, log-transformed data, and standardized data; results did not differ qualitatively between the data types, and therefore, we only present the analyses of raw data. All data analyses were carried out in the programming environment R, version 4.0.3 (R Core Team, 2020), using packages “car” v.3.0–12 (Fox et al., 2020), “lessR” v.4.0.8 (Gerbing, 2021), “BBmisc” v.1.11 (Bischof et al., 2017), “CCA” v.1.21 (González and Déjean 2012), “CCP” v.1.1 (Menzel, 2012), “gridExtra” v.2.3 (Auguie, 2017), and “ggplot2” v.3.3.5 (Wickham, 2016).

3 | RESULTS

We explored variation in six morphological variables for our 27 study species using MANOVAs and CCAs. Using the extremely conservative Bonferroni correction for *p*-values with *N* = 27, morphology in five species (Ochre-bellied flycatcher, plain antvireo (*Dysithamnus mentalis*), crowned woodnymph (*Thalurania colombica*), bicolored antbird (*Gymnophrys bicolor*), and band-tailed barbtroop (*Threnetes ruckeri*) showed a statistically significant relationship with elevation (*p* ≤ .05/27, or 0.00185) (Table 2). Using a less conservative Benjamini–Hochberg false-discovery-rate correction with α = 0.05, three additional species (checker-throated stipplethroat (*Epinecrophyllos fulviventris*), white-whiskered hermit (*Phaethornis*

TABLE 1 Study species. 27 species representing three orders and eleven families were included in this dataset. Elevational range represents the span between the highest and lowest captures of the species in this study

Species	Scientific name	Family	Sample size	Elevational range (m)
Ochre-bellied flycatcher	<i>Mionectes oleagineus</i>	Tyrannidae	342	675
Bicolored antbird	<i>Gymnophrys bicolor</i>	Thamnophilidae	262	440
White-whiskered hermit	<i>Phaethornis yaruqui</i>	Trochilidae	243	440
White-bearded manakin	<i>Manacus manacus</i>	Pipridae	194	440
Long-billed hermit	<i>Phaethornis longirostris</i>	Trochilidae	178	440
Orange-billed sparrow	<i>Arremon aurantirostris</i>	Passerellidae	173	440
Plain-brown woodcreeper	<i>Dendrocincla fuliginosa</i>	Furnariidae	171	440
Crowned woodnymph	<i>Thalurania colombica</i>	Trochilidae	141	440
Gray-and-gold warbler	<i>Myiothlypis fraseri</i>	Parulidae	130	675
Orange-bellied euphonia	<i>Euphonia xanthogaster</i>	Fringillidae	124	400
Green-crowned brilliant	<i>Heliodoxa jacula</i>	Trochilidae	120	440
Band-tailed barbtthroat	<i>Threnetes ruckeri</i>	Trochilidae	115	440
Blue-black grosbeak	<i>Cyanoloxia cyanoides</i>	Cardinalidae	113	440
Slaty antwren	<i>Myrmotherula schisticolor</i>	Thamnophilidae	106	440
Wedge-billed woodcreeper	<i>Glyphorhynchus spirurus</i>	Furnariidae	96	440
Olive-striped flycatcher	<i>Mionectes olivaceus</i>	Tyrannidae	82	440
Violet-bellied hummingbird	<i>Chlorestes julie</i>	Trochilidae	75	440
Chestnut-backed antbird	<i>Poliocrania exsul</i>	Thamnophilidae	72	440
Checker-throated stipplethroat	<i>Epinecrophylia fulviventris</i>	Thamnophilidae	69	420
Plain antvireo	<i>Dysithamnus mentalis</i>	Thamnophilidae	67	675
Scale-crested pygmy-tyrant	<i>Lophotriccus pileatus</i>	Tyrannidae	64	675
Black-crowned antshrike	<i>Thamnophilus atrinucha</i>	Thamnophilidae	59	440
Sulphur-rumped flycatcher	<i>Myiobius sulphureipygius</i>	Tityridae	57	440
White-throated spadebill	<i>Platyrinchus mystaceus</i>	Tyrannidae	55	440
Bay wren	<i>Cantorchilus nigricapillus</i>	Troglodytidae	54	440
White-whiskered puffbird	<i>Malacoptila panamensis</i>	Bucconidae	52	440
White-tipped sicklebill	<i>Eutoxeres aquila</i>	Trochilidae	49	440

yaruqui), and white-bearded manakin (*Manacus manacus*)) showed a correlation between morphology and elevation. Results were consistent between CCAs and MANOVAs, down to the level of statistical significance (Table 2 & Table S1).

The regressions between individual morphological variables and elevation were generally not statistically significant, with seven exceptions: tail-length covaried significantly with elevation in the ochre-bellied flycatcher and the band-tailed barbtthroat; bill-length covaried in the bicolor antbird; bill depth in the ochre-bellied flycatcher and bicolor antbird; and weight, in the crowned woodnymph and white-bearded manakin (Table 2). Loadings of the different morphological variables on the single canonical covariate similarly varied (Table S1). One or two variables had substantially the largest contributions for some species, such as the bicolor antbird (bill length and bill depth), and the white-bearded manakin (weight), both of which are the results consistent with those from the regressions. Conversely, the canonical covariate was strongly influenced by multiple variables for other species, including the

white-whiskered hermit and the plain antvireo. No single morphological variable loaded strongly onto the canonical covariate for every species, even among the eight listed above for which morphology and elevation had a statistically significant relationship overall. The square of the canonical correlation, analogous to an R^2 value in a linear regression, varied from 0.0183 (slaty antwren) to 0.374 (plain antvireo) (Table S1, Figures 2-4).

To account for the possibility that the patterns we found were driven by spatial segregation in age or sex classes, we explored whether age and sex varied with elevation in the subset of species that showed a relationship between morphology and elevation. Most of these species pose challenges for accurate assessment of age and/or sex in the field in the absence of reproductive characters; sample sizes for age and sex were therefore lower, but still above 50. Age and sex were assessed in the field based on the Wolfe-Ryder-Pyle system (Wolfe et al., 2010). For the eight species with statistically significant relationships between morphology and elevation, we performed MANOVAs assessing the relationship between

TABLE 2 MANOVA and regression results

Species	Wing chord		Tail length		Bill length		Bill width		Bill depth		Weight		Overall	
	R ²	p-val.	R ²	p-val.	R ²	p-val.	R ²	p-val.	R ²	p-val.	R ²	p-val.	R ²	p-val.
Slaty antwren	-0.009	0.701	0.010	0.167	-0.010	0.706	-0.010	0.681	-0.011	0.900	-0.010	0.737	0.970	
Ochre-bellied flycatcher	0.010	0.039	0.026	0.003	0.006	0.089	-0.001	0.412	0.022	0.005	0.003	0.171	0.000	
Plain antvireo	0.063	0.026	0.024	0.119	0.076	0.023	-0.018	0.848	-0.015	0.655	0.062	0.029	0.001	
Orange-bellied euphonia	0.003	0.248	0.001	0.293	-0.009	0.625	-0.009	0.660	-0.011	0.934	0.025	0.050	0.751	
Checker-throated stipplethroat	-0.008	0.486	0.055	0.041	0.061	0.032	-0.015	0.695	-0.013	0.642	0.002	0.297	0.010	
Olive-striped flycatcher	-0.013	0.819	-0.013	0.892	-0.014	0.876	0.037	0.054	-0.013	0.858	0.002	0.283	0.589	
Black-crowned antshrike	0.061	0.039	0.035	0.101	0.033	0.118	0.017	0.192	0.169	0.003	0.067	0.033	0.148	
Crowned woodnymph	0.013	0.101	0.026	0.034	-0.006	0.590	0.056	0.004	0.001	0.285	0.078	0.001	0.001	
White-whiskered hermit	0.025	0.009	-0.004	0.739	0.035	0.004	0.016	0.036	0.008	0.102	0.001	0.293	0.010	
Green-crowned brilliant	0.049	0.011	0.013	0.124	0.029	0.049	-0.003	0.393	-0.009	0.728	0.004	0.226	0.639	
White-throated spadebill	-0.023	0.960	-0.022	0.873	-0.025	0.916	0.074	0.046	-0.008	0.413	-0.011	0.483	0.490	
Bicolored antbird	-0.004	0.727	-0.002	0.462	0.077	0.000	-0.002	0.468	0.035	0.005	-0.004	0.700	0.000	
Violet-bellied hummingbird	0.001	0.311	0.025	0.099	-0.005	0.438	0.035	0.061	0.104	0.003	-0.016	0.802	0.590	
Sulphur-rumped flycatcher	0.000	0.319	0.098	0.026	-0.025	0.977	-0.004	0.363	0.032	0.135	-0.001	0.328	0.333	
White-whiskered puffbird	-0.014	0.574	-0.006	0.404	0.065	0.050	0.031	0.127	0.010	0.236	-0.018	0.694	0.419	
White-tipped sicklebill	0.054	0.068	-0.018	0.614	0.108	0.021	0.018	0.196	-0.024	0.754	-0.013	0.503	0.115	
Band-tailed barthroat	0.046	0.014	0.124	0.000	-0.009	0.714	0.043	0.019	0.002	0.267	-0.008	0.634	0.000	
Wedge-billed woodcreeper	-0.012	0.938	-0.005	0.445	0.033	0.064	-0.010	0.624	-0.011	0.691	0.008	0.193	0.567	
Gray-and-gold warbler	-0.005	0.528	0.000	0.325	0.017	0.097	0.003	0.264	-0.007	0.578	0.028	0.033	0.378	
White-bearded manakin	0.003	0.207	-0.001	0.345	-0.006	0.823	0.002	0.243	0.012	0.085	0.056	0.001	0.006	
Blue-black grosbeak	-0.011	0.957	0.005	0.240	-0.007	0.518	0.026	0.079	0.007	0.219	0.003	0.246	0.085	
Plain-brown woodcreeper	0.018	0.052	0.018	0.057	-0.003	0.435	-0.006	0.729	0.010	0.111	0.004	0.212	0.251	
Chestnut-backed antbird	-0.014	0.789	-0.017	0.924	-0.013	0.643	-0.013	0.629	0.007	0.234	0.099	0.006	0.220	
Long-billed hermit	0.024	0.025	-0.006	0.772	0.002	0.253	-0.005	0.721	-0.006	0.747	-0.006	0.735	0.342	

(Continues)

TABLE 2 (Continued)

Species	Wing chord		Tail length		Bill length		Bill width		Bill depth		Weight		Overall	
	R ²	p-val.	R ²	p-val.	R ²	p-val.	R ²	p-val.	R ²	p-val.	R ²	p-val.	R ²	p-val.
Bay wren	-0.005	0.378	-0.020	0.739	-0.021	0.671	0.075	0.047	0.072	0.052	-0.020	0.731	0.133	
Orange-billed sparrow	-0.002	0.409	-0.001	0.340	-0.001	0.341	-0.007	0.825	0.001	0.281	-0.005	0.583	0.470	
Scale-crested pygmy-tyrant	-0.006	0.424	-0.011	0.543	0.017	0.162	0.011	0.208	-0.008	0.465	0.035	0.078	0.374	

Note: The table shows R² values and p-values for the relationship between each dependent variable and elevation, followed by an overall p-value. p-values significant after a Bonferroni correction with N = 27 are italicized and in bold, and shaded gray; p-values that were significant after a Benjamini–Hochberg false-discovery-rate correction ($\alpha = 0.05$) but not after a Bonferroni correction are in bold, and shaded light gray.

elevation, and age and sex, using both two and three age classes based on molt. None of these relationships approached statistical significance (data not shown).

We conducted two further checks to assess the robustness of our findings. First, for the four species also sampled at CJA (elevation: 25 m), we repeated our analyses with samples from that location omitted, to examine the possibility that our results were unduly influenced by elevational outliers. With these data omitted, correlations for the plain antvireo became only marginally significant ($p \sim .08$) in both forms of analyses; no other changes were seen (data not shown). Non-systematic observational data suggest that these species are resident at CJA also; thus, we only discuss the complete data set below. Second, we repeated our analyses separately for each year of data. These results were broadly consistent with the results from the undivided data: we found few changes in relative significance, but a decrease in significance across all results, as is expected for a smaller data set (data now shown).

4 | DISCUSSION

We found evidence that morphology covaried with elevation in eight species of the 27 we examined, along with a 675-m elevational gradient across a short horizontal distance in largely contiguous forest habitat (Figures 2–4). The morphometric characteristics that covaried with elevation differed substantially between species (Table S1). Covariance between environmental conditions and phenotype can constitute evidence of local adaptation and may be the best evidence available when reciprocal transplant experiments are intractable (Blanquart et al., 2012; Conover et al., 2009; Savolainen et al., 2013). Given the existence of substantial variation in habitat over this gradient, the covariance between elevation and morphology that we demonstrate constitutes preliminary evidence for the existence of adaptive variation in at least eight species in this system, and consequently of variance in selection pressure over a small spatial scale. Evidence for adaptive, or putatively adaptive, variation in morphology has been found along several tropical elevational gradients (Bertrand et al., 2016; Bulgarella et al., 2007; Gadek et al., 2018; Gutiérrez-Pinto et al., 2014; McCormack & Smith, 2008; Milá et al., 2009; Price, 1991; VanderWerf, 2012), and similar variation has been found using genetic or metabolic traits (Barve et al., 2016; Cheviron & Brumfield, 2009; Galen et al., 2015). To the best of our knowledge, however, no other study has demonstrated the existence of morphological variation within highly mobile species over a comparably small horizontal or elevational scale or in a comparably diverse suite of species.

We found no covariance between morphology and elevation in 19 species. This may indicate that these species do not experience variance in selection pressure, or alternatively that any divergence driven by selection is overwhelmed by gene flow (Lenormand, 2002). However, we believe further study is necessary to determine which species do not exhibit local adaptation given the substantial variation

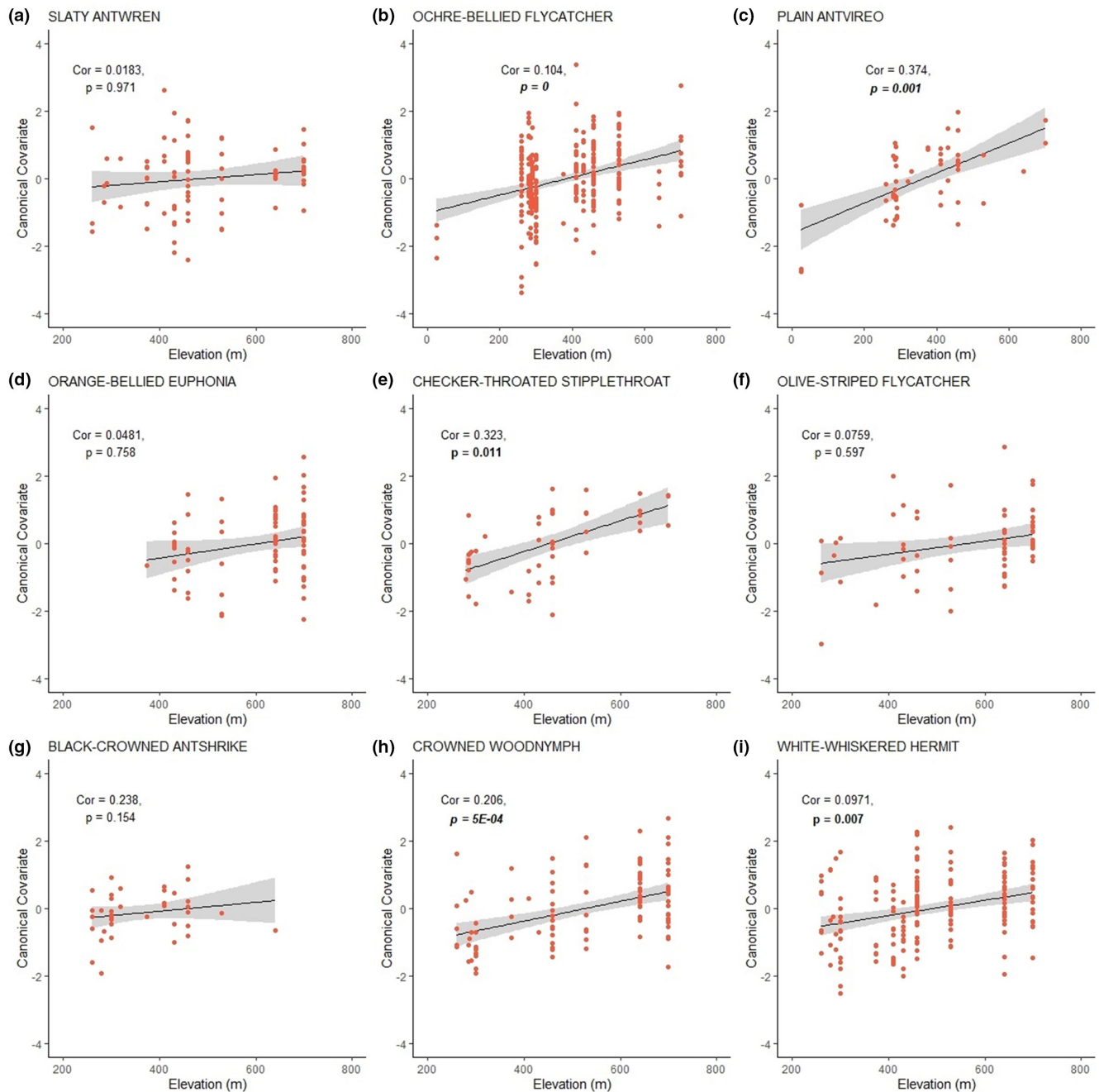


FIGURE 2 Plots of canonical covariate scores against elevation for species 1–9, of 27 (Slaty antwren (*Myrmotherula schisticolor*, a); ochre-bellied flycatcher (*Mionectes oleaginous*, b); plain antvireo (*Dysithamnus mentalis*, c); orange-bellied euphonia (*Euphonia xanthogaster*, d); checker-throated stipplethroat (*Epinecrophylia fulviventris*, e); olive-striped flycatcher (*Mionectes olivaceus*, f); black-crowned antshrike (*Thamnophilus atrinucha*, g); crowned woodnymph (*Thalurania colombica*, h); and white-whiskered hermit (*Phaethornis yaruqui*, i). Points represent individuals; lines represent the best-fit linear relationship with standard errors. “Cor” values are the squares of the canonical correlation, analogous to R^2 values. p -values based on 10,000 permutation tests are also shown. p -values significant after a Bonferroni correction with $N = 27$ are italicized and in bold; p -values that were significant after a Benjamini-Hochberg false-discovery-rate correction ($\alpha = 0.05$) but not after a Bonferroni correction are in bold

in sample size (52–361) in this dataset, and given that the four species with the largest sample sizes all showed a significant correlation. Further, at least one of the species for which we found no relationship between morphology and elevation, the wedge-billed woodcreeper (*Glyphorynchus spirurus*), has been demonstrated to exhibit

local adaptation along the much broader gradient on the Andean slopes (Milá et al., 2009). Nonetheless, our findings imply the existence of variation in the degree of adaptive divergence across taxa. As the focus of this paper is to examine the existence of morphological variability across clades in a geographically restricted area,

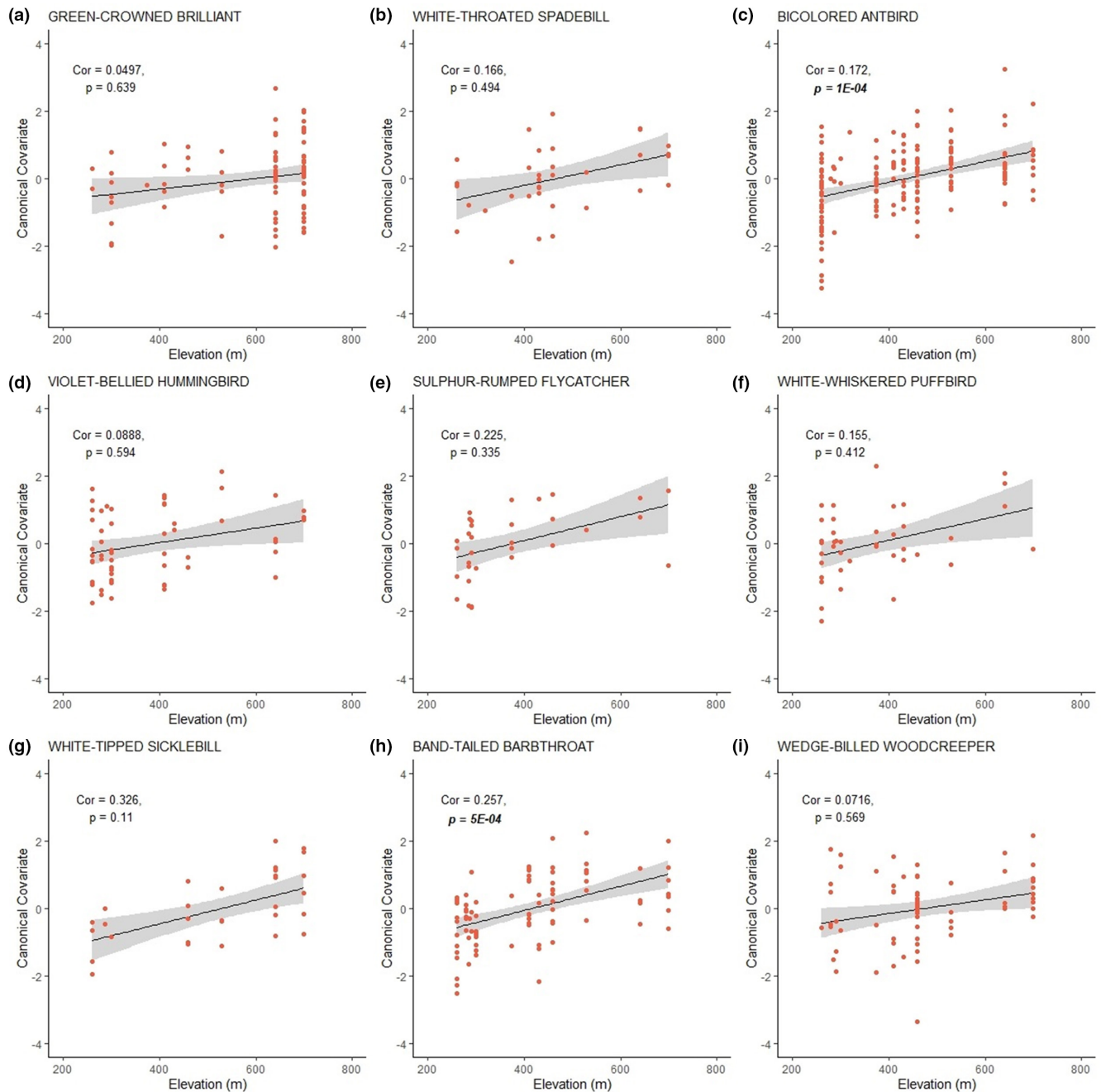


FIGURE 3 Plots of canonical covariate scores against elevation for species 10–18, of 27 (green-crowned brilliant (*Heliodoxa jacula*, a); white-throated spadebill (*Platyrinchus mystaceus*, b); bicolor antbird (*Gymnophaps bicolor*, c); violet-bellied hummingbird (*Chlorestes julie*, d); sulfur-rumped flycatcher (*Myiobius sulphureipygius*, e); white-whiskered puffbird (*Malacoptila panamensis*, f); white-tipped sicklebill (*Eutoxeres aquila*, g); band-tailed barbtroth (*Threnetes ruckeri*, h); and wedge-billed woodcreeper (*Glyphorhynchus spirurus*, i). Points represent individuals; lines represent the best-fit linear relationship with standard errors. “Cor” values are the squares of the canonical correlation, analogous to R^2 values. p -values based on 10,000 permutation tests are also shown. p -values significant after a Bonferroni correction with $N = 27$ are italicized and in bold; p -values that were significant after a Benjamini–Hochberg false-discovery-rate correction ($\alpha = 0.05$) but not after a Bonferroni correction are in bold

we did not attempt to quantify the extent of that variability or to compare it across species in a framework controlled for phylogeny. We note that the eight species in which we found a significant relationship between elevation and morphology span four families and two orders; it is therefore unlikely that the tendency for morphology

to covary with elevation is entirely driven by phylogeny. Phenotypic variation, including in morphological traits, may also be the product of plastic responses to varying environmental conditions (Price et al., 2003), and that plasticity may act in concert with, or in opposition to, selective pressure on the same traits (Conover et al., 2009).

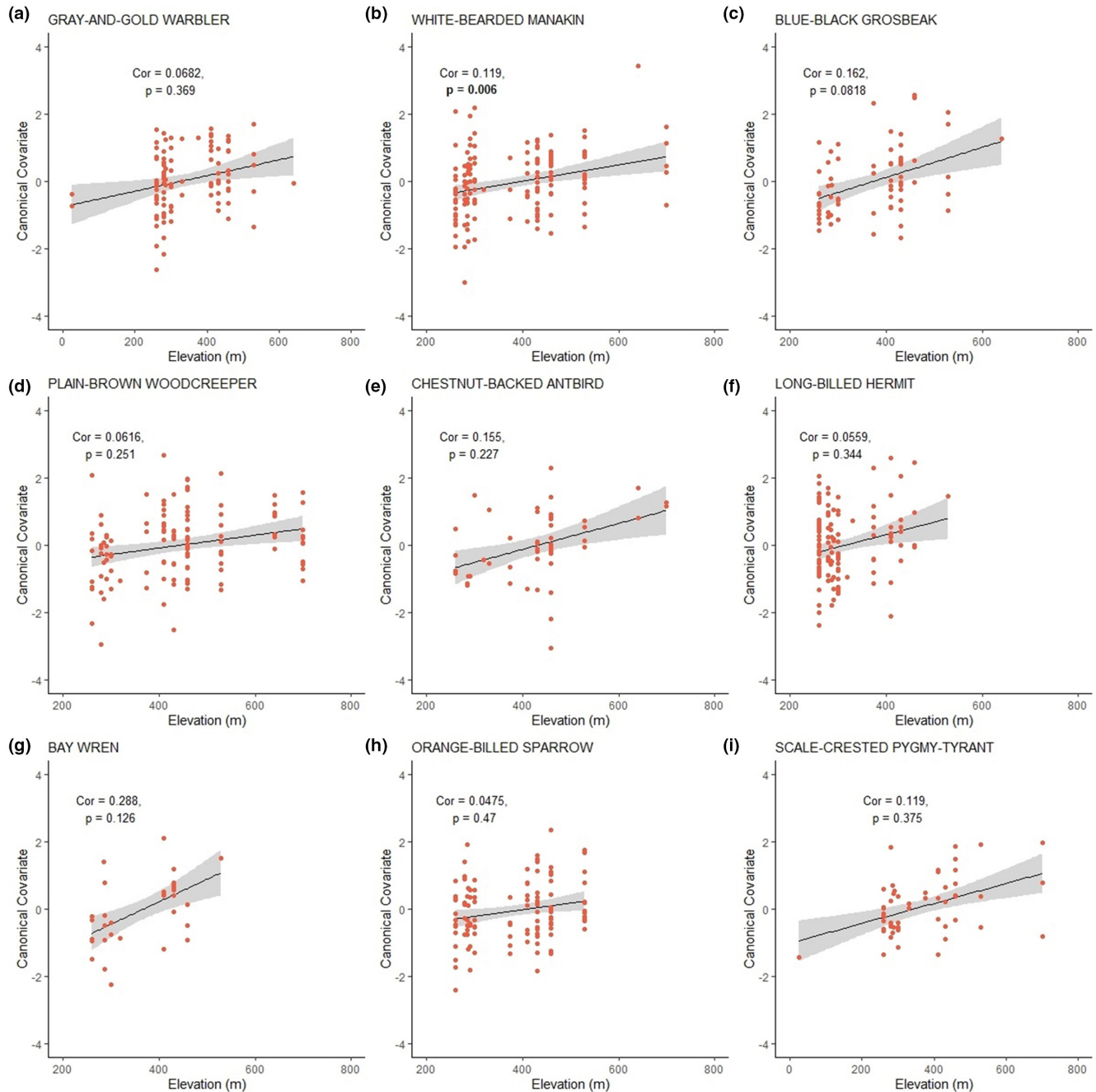


FIGURE 4 Plots of canonical covariate scores against elevation for species 19–27, of 27 (gray-and-gold warbler (*Myiothlypis fraseri*, a); white-bearded manakin (*Manacus manacus*, b); blue-black grosbeak (*Cyanoloxia cyanoide*, c); plain-brown woodcreeper (*Dendrocincla fuliginosa*, d); chestnut-backed antbird (*Poliocrania exsul*, e); long-billed hermit (*Phaethornis longirostris*, f); bay wren (*Cantorchilus nigricapillus*, g); orange-billed sparrow (*Arremon aurantirostris*, h); and scale-crested pygmy-tyrant (*Lophotriccus pileatus*, i). Points represent individuals; lines represent the best-fit linear relationship with standard errors. “Cor” values are the squares of the canonical correlation, analogous to R^2 values. p -values based on 10,000 permutation tests are also shown. p -values significant after a Bonferroni correction with $N = 27$ are italicized and in bold; p -values that were significant after a Benjamini–Hochberg false-discovery-rate correction ($\alpha = 0.05$) but not after a Bonferroni correction are in bold

Disentangling the relative contributions of plasticity and adaptive divergence requires comparing phenotypic and genotypic divergence and is outside the scope of this manuscript.

Several drivers of elevational variation in selection pressure have been documented in other systems and species. Prominent among

these is the cost of thermoregulation in colder temperatures, as articulated in Bergmann's and Allen's rules; evidence for this type of selection along elevational gradients is widespread (Gutiérrez-Pinto et al., 2014; VanderWerf, 2012), but not uniform (Freeman, 2017). Hypoxic environments at high altitudes are also known to drive

divergence in related phenotypic traits, including hemoglobin concentration (Barve et al., 2016) and hemoglobin function (Galen et al., 2015). Although two of our species (crowned woodnymph and white-bearded manakin) show positive correlations between weight and elevation, we believe both these known drivers of adaptive divergence are unlikely to be significant to our system, given its tropical climate and small elevational span of 675 m, with a maximum elevation of 700 m above sea level. Selection pressures related to foraging, found to drive altitudinal morphological divergence elsewhere, are likely more relevant in this system. For instance, in *Phylloscopus* warblers in the Himalayas, beak size relative to tarsus length covaries with elevation and also with habitat (Price, 1991); tarsus length and beak size relative to body size covaries with elevation, and with the quantity of moss on tree trunks, in the wedge-billed woodcreeper (*Glyphorhynchus spirurus*) (Milá et al., 2009); bill shape covaries with elevation, and diet, in the Mexican jay (*Aphelocoma ultramarina*) (McCormack & Smith, 2008).

We found considerable variation in which traits contributed most strongly to morphological covariance with elevation (Table S1), although bill shape appears to be among the relevant traits in at least two species. Species ecology is also known to strongly affect the extent of gene flow between populations (Burney & Brumfield, 2009; Harvey et al., 2017), including when populations are separated in space but not by large barriers to gene flow (Miller et al., 2020), although variation in levels of gene flow may or may not be relevant at the scale of this system. Species ecology is therefore likely to affect if and how morphology covaries with environment. The morphological variation we identified provides an opportunity to examine which aspects of species or habitat ecology may be driving adaptive divergence more generally in this system.

In conclusion, we found evidence of morphological variation along a short elevational gradient and short horizontal distance in eight species from four families out of the 27 species we examined. The features of morphology that covaried with elevation were strongly species-dependent. These results provide a foundation for examining local adaptation, adaptive divergence, and variation in selection pressure along tropical elevational gradients.

AUTHOR CONTRIBUTIONS

AL and ME involved in conceptualization, investigation, methodology, and writing—review and editing. All authors involved in data curation. AL (lead) and ME (supporting) involved in formal analysis. ME, HG, EF, and CAPG involved in data collection. ME (lead), HG, EF, and CAPG (supporting) involved in project administration. ME involved in resources. AL performed visualization. AL involved in writing—original draft.

ACKNOWLEDGMENTS

This study was conducted as a part of the project “Diversidad genética y conservación de aves en el noroccidente de Ecuador”: we are grateful to Jordan Karubian and Elisa Bonaccorso for allowing us to use the data generated during this project. Data collection was authorized by permit MAE-DNB-CM-2015-0017 from the Ministerio

del Ambiente del Ecuador, granted to the Universidad Tecnológica Indoamérica, and permit MAE-UAF-DPAM-2018-1395-E, granted to the Corporación Grupo Ecológico Jama-Coaque. We would like to thank Trevor D. Price for assistance with the methods, John Bates, Elisa Bonaccorso, Laura Cespedes, and two anonymous reviewers for helpful comments on the manuscript, and Nick Crouch for assistance with analyses. We would also like to thank Third Millennium Alliance team members Edilberto Márquez, Dany Murillo, Annie Meyer, Sasha Robinson, the interns who helped collect the data used in this research, and Ryan Lynch, for helping organize and maintain this project and this data set. We thank Steve Albert and the Institute for Bird Populations for equipment donations. Work by HG, EF, CAPG, and ME was supported by institutional funding from the Third Millennium Alliance; AL was supported by institutional funding from the University of Chicago and the Field Museum.

CONFLICT OF INTEREST

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.2547d7wsm> (Lele et al., 2022).

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How to cite this article: Lele, A., Garrod, H. M., Ferguson, E., Azahara Prieto Gil, C. & Ellis, M. (2022). Variation in avian morphology along a short tropical elevational gradient. *Biotropica*, 00, 1–12. <https://doi.org/10.1111/btp.13110>