

# Molecular and morphological differentiation among Torrent Duck (*Merganetta armata*) populations in the Andes

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## Abstract

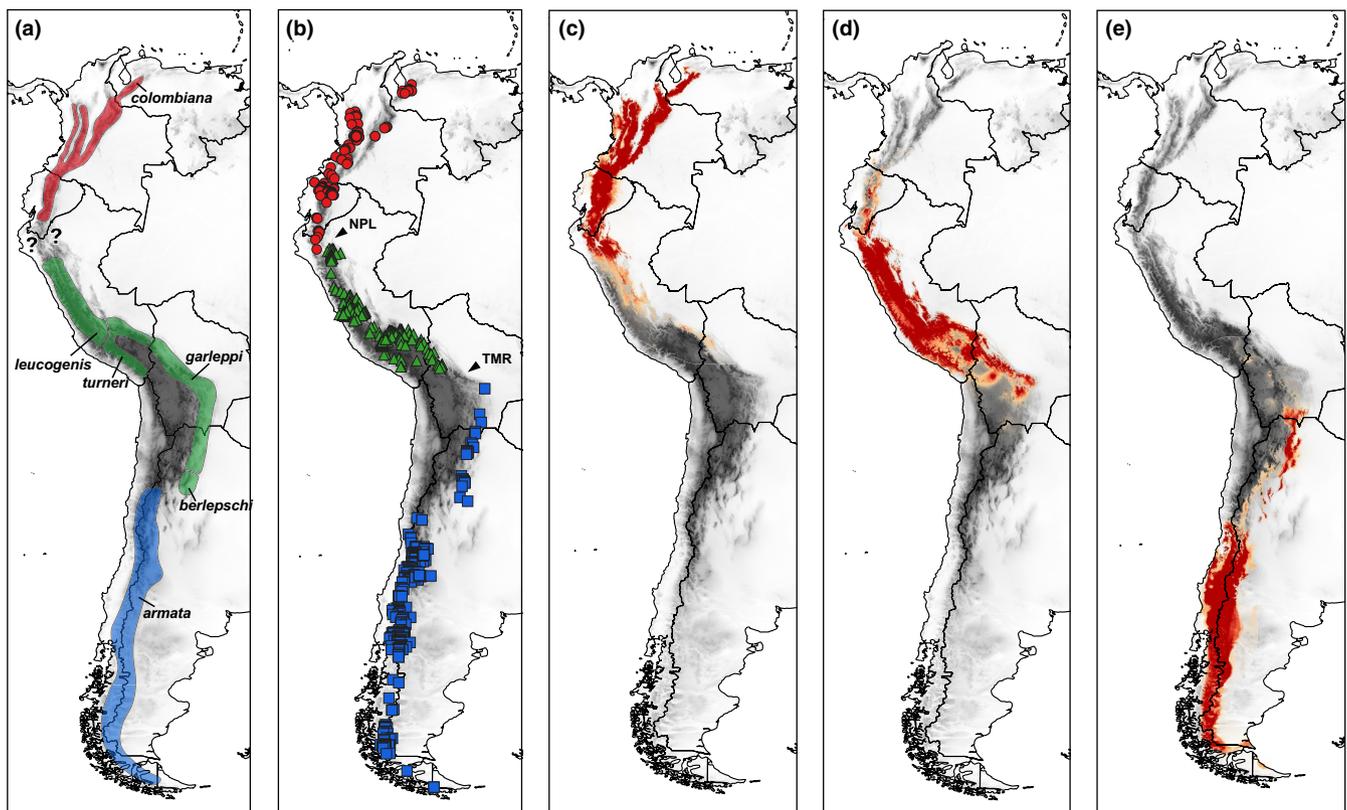
Birds living in riverine environments may show weak population structure because high dispersal abilities required to track habitat dynamics can result in gene flow over broad spatial scales. Alternatively, the configuration of river networks may result in restricted dispersal within river courses or basins, leading to high genetic structure. Although several bird species are riverine specialists in the Andes, no study has extensively evaluated the population genetic structure of any of them. We examined evidence from genetic and morphological data to address questions about the biogeography and taxonomy of the Torrent Duck (*Merganetta armata*), a riverine specialist bird with a broad distribution in Andean riverine habitats which certainly comprises different subspecies and may comprise more than one species. We found deep subdivisions of Torrent Duck populations from the northern, central and southern portions of the Andes. These lineages, which partly coincide with subspecies described based on plumage variation and body size, do not share mtDNA haplotypes, have private nuclear alleles and exhibit marked differences in morphometric traits. Some geographic barriers presumably restricting gene flow between groups partially coincide with those associated with major genetic breaks in forest species with similar distributions along the Andes, suggesting that bird assemblages including species occupying different habitats were likely affected by common biogeographical events. The three groups of Torrent Ducks may be considered different species under some species definitions and are distinct evolutionary lineages to be conserved and managed separately.

## 1 | INTRODUCTION

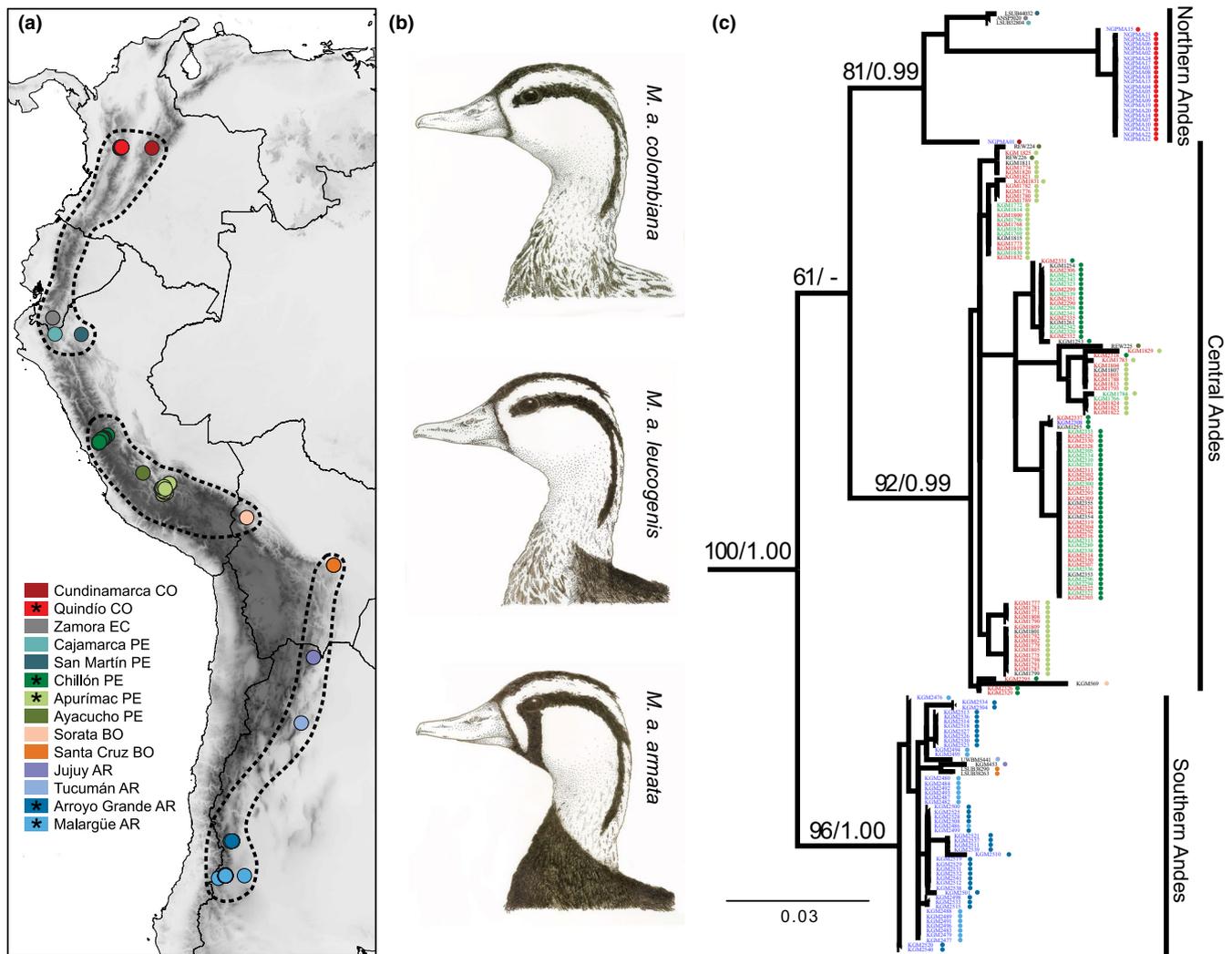
Why are tropical montane regions like the Andes hotspots of global biodiversity? Substantial effort has been devoted to understand the origin and maintenance of species diversity in the Andes, with researchers arguing that one must consider the role of evolutionary and historical processes (i.e., speciation, extinction and colonization) to fully comprehend the high richness and endemism of the region (Fjeldså, Bowie, & Rahbek, 2012; Graham et al., 2014; Quintero & Jetz, 2018; Rull, 2011). The elongated shape and intricate topography of the Andes Mountains have contributed to the fragmentation of species ranges, thereby facilitating geographic isolation, population divergence and ultimately speciation (Graves, 1988; Pennington et al., 2004; Remsen, 1984; Vuilleumier, 1969). Most of the evidence supporting this idea in birds comes from phylogeographic studies of terrestrial species, which reveal that gene flow among populations is limited by major barriers in the Andes such as the Marañón River Valley in

Peru, the Táchira Depression in Venezuela or the Magdalena River Valley in Colombia (Cadena, Klicka, & Ricklefs, 2007; Gutiérrez-Pinto et al., 2012; Miller, Bermingham, Ricklefs, & Klicka, 2007; Pérez-Emán, 2005; Valderrama, Pérez-Emán, Brumfield, Cuervo, & Cadena, 2014; Weir, Bermingham, Miller, Klicka, & González, 2008). Divergence across such barriers in phenotypic traits important for speciation (i.e., plumage or song) thus often occurs in geographic isolation as a consequence of genetic drift or of various forms of selection (Benham & Witt, 2016; Cadena, Cheviron, & Funk, 2011; Winger, 2017; Winger & Bates, 2015).

Riverine environments may affect the dispersal and hence population structure of their inhabitants in different ways. First, because these environments are highly dynamic and sometimes ephemeral, and prone to ecological disturbance either manmade or natural, they may promote high dispersal abilities in birds needing to track relatively rapid changes in habitat, resulting in weak population structure (Cadena, Gutiérrez-Pinto, Dávila, & Chesser, 2011; Harvey, Aleixo,



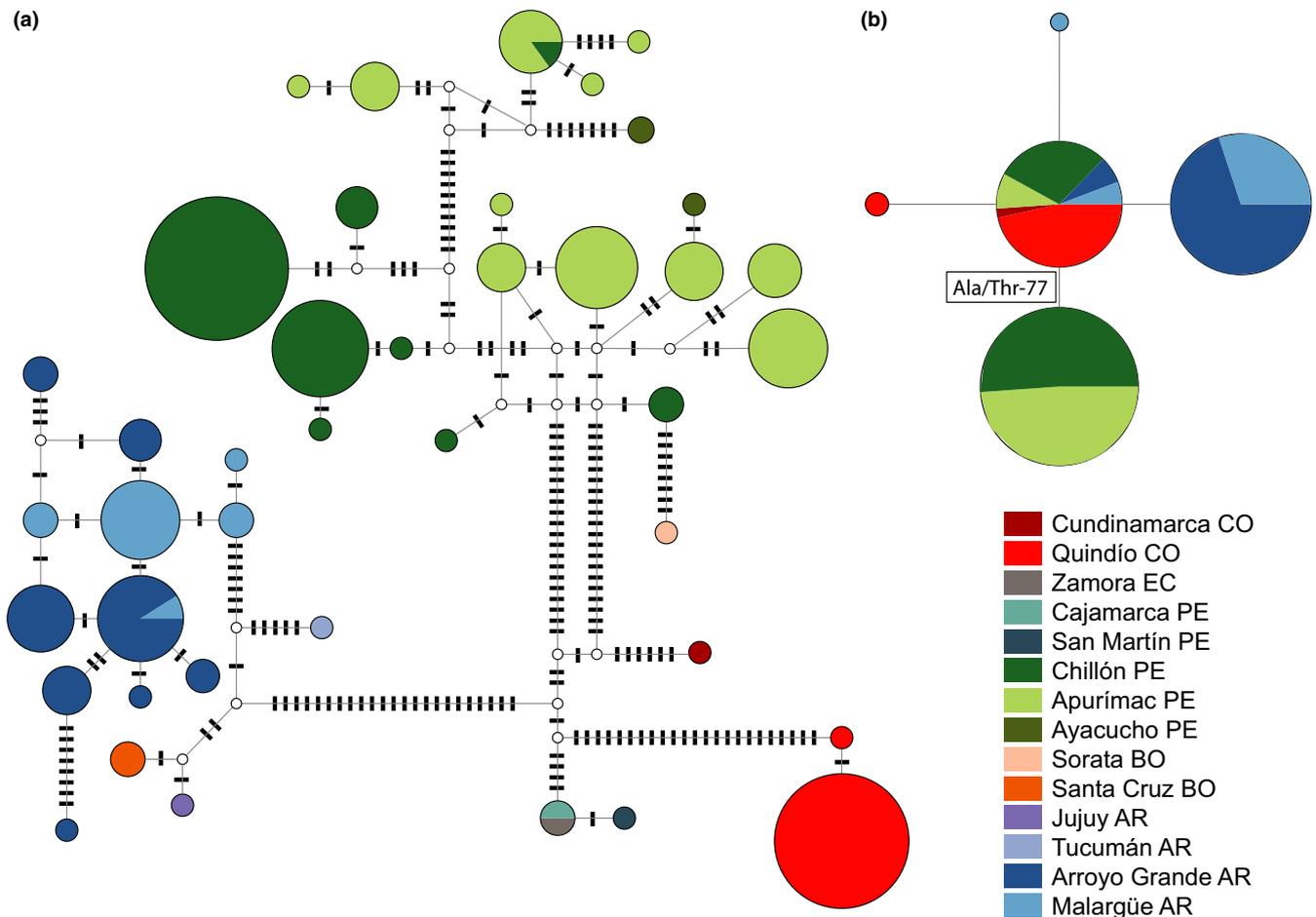
**FIGURE 1** (a) Geographic distribution of Torrent Duck subspecies following Callaghan (1997), with *colombiana* in red, *leucogenis* in green and *armata* in blue. The question marks between the ranges of *colombiana* and *leucogenis* denote the uncertainty about distributional limits for these two taxa. The *leucogenis* range is further subdivided into the four taxa originally described, following Phillips (1926). (b) Occurrence data of Torrent Ducks in the Andes extracted from the GBIF database (see Appendix S1 for details), where red dots, green triangles and blue squares identify the samples classified into Northern, Central or Southern Andes clades, respectively. Arrows indicate the location of two possible barriers to gene flow in Torrent Ducks, namely the North Peruvian Low (NPL) and the Turner Mountain Range (TMR). Owing to uncertainty in the geographic limits of populations, we show models of the potential distribution of the Northern (c), Central (d) and Southern Andes groups (e) identified using molecular analyses. Potential distributions were modelled using climatic data and the software Maxent as described in Appendix S1. Warmer colours indicate higher probability of presence



**FIGURE 2** (a) Map of the localities (dots) where individual Torrent Duck samples were obtained for DNA and morphological analyses, grouped according to the three major clades obtained with mtDNA data (delineated by dashed lines). Those localities marked with an asterisk were the heavily sampled rivers, as described in the methods section. For more details refer to Appendix S1. (b) Morphological variation in Torrent Ducks in the coloration patterns of male heads characteristic of each main clade recovered by the phylogenetic analysis (Illustrations by Fernando Vargas-Salinas). (c) mtDNA control-region topology obtained with the maximum-likelihood analysis, showing bootstrap support values and posterior probabilities above main branches. The HBA2 allele for position 77 in the amino acid sequence for each individual is mapped on the phylogeny with colours blue (Ala/Ala), red (Thr/Thr), green (Ala/Thr) and black (no data). Samples in (a) and (c) are coloured by locality and are the same as in Figure 3

Ribas, & Brumfield, 2017; Medina, Cooke, & Ord, 2018; Smith et al., 2014). Alternatively, the configuration of river networks may result in restricted dispersal within river courses or basins, leading to high genetic structure (Fetzner & Crandall, 2003, see references in Chaput-Bardy, Fleurant, Lemaire, & Secondi, 2009). Although several bird species are riverine specialists in the Andes (Buckton & Ormerod, 2002), no study has extensively evaluated the population genetic structure of any of them. More broadly, phylogeographic work on riverine species of birds from other Neotropical regions such as the Amazon basin is remarkably scarce (Areta, Dornas, Kirwan, Araújo-Silva, & Aleixo, 2017; Choueri et al., 2017; Thom et al., 2018).

The Torrent Duck (*Merganetta armata*: Anatidae) lives in fast-flowing Andean rivers from the Cordillera de Mérida (Venezuela) to Tierra del Fuego (Argentina) at elevations ranging from sea level at higher latitudes to more than 4,500 m in the Central Andes (Figure 1; Carboneras, 1992). In addition to occupying a broad elevational range, this species can be found in rivers characterized by a wide variety of conditions, ranging from highly seasonal and cool habitats (i.e., in southern Argentina) to tropical, warm and humid climates (i.e., in the Colombian Andes), as well as very dry areas (i.e., the Peruvian coast). The broad distribution and strict specialization on riverine habitats of Torrent Duck makes it an ideal model to study population structure of Andean river-specialist birds.



**FIGURE 3** mtDNA (a) and HBA2 (b) haplotype networks showing in different colours the association with geographic location of each sample. Circle size shows the frequency of each haplotype, empty small circles represent unsampled haplotypes, and bars indicate single mutational steps between haplotypes

Torrent Ducks, the only species in its genus, exhibit geographic variation in plumage and body size, with at least three subspecies currently recognized (Figures 1a and 2b and Figure S1): (a) *M. a. colombiana* in Venezuela, Colombia and Ecuador; (b) *M. a. leucogenis* in Peru, Bolivia and north-western Argentina; and (c) *M. a. armata* in Chile and Argentina. There has been some disagreement about taxon and distribution limits in the group (Callaghan, 1997; Conover, 1943; Johnsgard, 1966), with researchers raising the possibility that different populations may be considered distinct species (Callaghan, 1997), or a single species comprising as many as seven subspecies. As originally described (summarized by Phillips, 1926 and Conover, 1943), the range of *colombiana* extended south to central Ecuador (around Chimborazo), with *leucogenis*, *turneri*, *garleppi* and *berlepschi* successively replacing each other from south of the North Peruvian Low to northern Argentina (Figure 1a), and *armata* occupying the Argentinean and Chilean Andes south from Mendoza. The current consensus (after Johnsgard, 1966; Figure 1a) considers only three subspecies, lumping *leucogenis*, *turneri*,

*garleppi* and *berlepschi* into the *leucogenis* group. Moreover, distribution limits between taxa have been repeatedly debated. Some authors extend the range of *colombiana* south to central Ecuador (Conover, 1943; Phillips, 1926) or to the Ecuador-Peru border (Callaghan, 1997), but never overlapping with *leucogenis*; incomplete geographic sampling of specimens has prevented the establishment of clear distribution limits between these two taxa (Figure 1a). Similarly, although the only known gap in the range of Torrent Ducks is in the Bolivian altiplano, several authors have raised the possibility of a contact zone between *leucogenis* and *armata* in northern Argentina. Apart from a preliminary analysis delimiting the geographic ranges of subspecies in which the author called for an urgent re-analysis of the systematics and distribution boundaries of taxa (Callaghan, 1997), no recent formal systematic revision exists for this species.

We recently completed an analysis of geographic variation in external morphology of Torrent Ducks, which revealed morphometric variation partly attributable to plasticity or adaptation to contrasting temperature regimes (Gutiérrez-Pinto

et al., 2014). However, information on geographic variation in phenotype has not been integrated with molecular data to address questions about the biogeography and taxonomy of Torrent Ducks. Nonoverlapping patterns of phenotypic variation can be especially informative about species limits when populations overlap in geographic space (Zapata & Jimenez, 2012), or when individuals from two largely allopatric populations meet in areas connected by suitable environments (Cadena & Cuervo, 2010). Here, we thus jointly examine data from genetic and morphological sources to examine patterns of variation among Torrent Duck populations across their range from Colombia to Argentina. Our analyses allowed us to (a) assess whether patterns in population structure of this river specialist differ or not from those of codistributed forest birds in the Andes and (b) evaluate evidence in favour of or against the hypothesis that Torrent Duck populations may represent different species.

## 2 | METHODS

### 2.1 | Sampling and laboratory procedures

We used mist nets to capture Torrent Ducks in the field to obtain samples for genetic analyses and morphological measurements between 2010 and 2012 in five different rivers (Figure 2a and Table S1): (a) Río Quindío, Quindío, Colombia (1,500–2,100 m; 8 females and 15 males); (b) Río Pachachaca, Apurímac, Peru (2,200–3,600 m; 20 females and 28 males); (c) Río Chillón, Lima, Peru (1,000–4,000 m; 14 females and 48 males); (d) Arroyo Grande, Mendoza, Argentina (1,800–3,200 m; 16 females and 30 males); and (e) Río Malargüe, Mendoza, Argentina (1,600–1,900 m; 7 females and 14 males; Alza et al., 2017). Additional samples of specimens from Ecuador, Peru, Bolivia and Argentina were obtained from the tissue collections of the University of Alaska Museum, Louisiana State University Museum of Natural Science, the Academy of Natural Sciences of Philadelphia and the Burke Museum of Natural History and Culture, allowing us to expand geographic sampling (Figure 2a and Table S1).

For each captured duck, we took a blood sample from the basilic or ulnar veins and conserved it in lysis buffer and/or liquid nitrogen. Genomic DNA was extracted from total blood using either a DNeasy Blood & Tissue Kit (Qiagen), following a modified protocol (McCracken & Sorenson, 2005) or a phenol–chloroform method (Gutiérrez-Pinto et al., 2012). We first sequenced a fragment (635–644 bp) of the non-coding control region of mitochondrial DNA, a putatively neutral marker commonly used in phylogeographic analyses. We also assayed genetic variation in a fragment (379 bp) of the  $\alpha$ A subunit of the major haemoglobin gene (HBA2) spanning two exons and two introns, a protein-coding region important for adaptation to high-altitude hypoxia

in birds including waterfowl (McCracken, Barger, Bulgarella, Johnson, Sonsthagen, et al., 2009; McCracken & Sorenson, 2005; Natarajan et al., 2015). Previous work revealed evidence seemingly consistent with the hypothesis that adaptive evolution in the haemoglobin protein may exist in association with occupation of a wide range of elevations (Southern Andes: 0–4,000 m; Central Andes: 1000–4,500 m; Northern Andes 1,500–3,500 m) in Torrent Ducks (McCracken, Barger, Bulgarella, Johnson, Sonsthagen, et al., 2009). However, we do not interpret patterns of HBA2 variation in the context of adaptive evolution because (a) experimental evidence documenting functional differences in observed substitutions is lacking, and (b) Torrent Ducks sampled at all elevations (low and high) exhibited the same relatively high Hb-O<sub>2</sub> affinity, comparatively left-shifted to low-altitude waterfowl populations (Natarajan et al., 2015). Thus, our analyses of the biparentally inherited nuclear HBA2 and the maternally inherited control region served to provide complementary insights from neutral and functionally important loci about the biogeographical history of species (Lozano-Jaramillo, McCracken, & Cadena, 2018).

PCR protocols followed standard procedures to amplify HBA2 (McCracken, Barger, Bulgarella, Johnson, Sonsthagen, et al., 2009) and the control region (McCracken & Sorenson, 2005). We initially used overlapping primer pairs L78–H774 (Sorenson, Ast, Dimcheff, Yuri, & Mindell, 1999; Sorenson & Fleischer, 1996), but after careful examination of the sequences, we determined that our initial PCR products resulted in the amplification of nuclear mtDNA pseudogenes (numts; e.g., Sorenson & Quinn, 1998). Therefore, after analysing sequences, we redesigned a 5' forward primer L100-*Merganetta* (CATACATTTATGCGCCCCATAC) to selectively amplify true mtDNA sequences.

### 2.2 | Phylogeography

We began by reconstructing the evolutionary relationships and biogeographical history of populations using phylogenetic analyses of 198 control region sequences (Table S1) together with 12 additional sequences included as outgroups. Although there has been some speculation regarding the phylogenetic affinities of Torrent Ducks (Johnsgard, 1966), information about its sister group is limited because this species was not included in the most comprehensive molecular systematic analysis of the Anatidae (Gonzalez, Düttmann, & Wink, 2009), and was only treated as an outgroup in an analysis of the relationships among some endemic South American ducks (Bulgarella, Sorenson, Peters, Wilson, & McCracken, 2010). Furthermore, *Merganetta* is a monotypic genus and genetically distant from other waterfowl genera. For these reasons and following Bulgarella et al. (2010), we considered as outgroups seven species from three genera closely related to Torrent Ducks: *Tadorna tadorna* (GenBank

accession AY112962.1), *T. tadornoides* (AY112963.1), *Alopochen aegyptiacus* (AY112964.1), *Chloephaga poliocephala* (KC109006), *C. picta picta* (KC109015), *C. picta leucoptera* (KC109044), *C. rubidiceps* (KC109056) and *C. melanoptera* (KC109075). Also, because nuclear mitochondrial pseudogenes (numts) have proven useful as outgroups for phylogenetically isolated taxa (Bensasson, Zhang, Hartl, & Hewitt, 2001; Hay, Sarre, & Daugherty, 2004), we included sequences of mtDNA numts obtained from four Torrent Duck individuals (REW 225: GenBank accession MH806443; LSU B38290: MH806444; ANSP 5020: MH806445; and KGM 453: MH806446). We reasoned that if the pseudogenization event took place in the stem lineage leading to current *Merganetta* populations and their most recent common ancestor, numt sequences might serve as closer outgroup sequences compared with true mtDNA sequences from the more distantly related waterfowl genera *Tadorna*, *Alopochen* or *Chloephaga*. As expected, no numt sequence was included in the ingroup after conducting the phylogenetic analyses, and paralogous numt sequences were genetically more similar to *Merganetta* mtDNA sequences than orthologous sequences from the selected outgroup genera (i.e., all sequences originating from Torrent Ducks were monophyletic).

Sequences were aligned using the Geneious alignment algorithm implemented in Geneious v.5.4. (Drummond et al., 2011). We used ModelTest 3.7 (Posada & Crandall, 1998) and MrModelTest 2.3 (Nylander, 2004) together with PAUP\* 4.0b10 (Swofford, 2002) to select the nucleotide substitution model that best fit the data, which was GTR + I+ $\Gamma$ . We ran a maximum-likelihood analysis using RAxML 7.0.4 (Stamatakis, 2006) and established statistical support for branches using 1,000 bootstrap replicates. We also conducted a Bayesian inference analysis using MrBayes v.3.2 (Ronquist & Huelsenbeck, 2003) with four MCMC chains ran for 20 million generations, sampling trees every 2,000 generations and discarding the first 2,500 trees as burn-in. To further visualize relationships between different populations, we built a haplotype network using the median-joining algorithm implemented in Network v.4.6 (Bandelt, Forster, & Rohl, 1999).

### 2.3 | Haemoglobin (HBA2) characterization

After sequencing the HBA2 fragment, we defined the gametic phase of the heterozygous sites using PHASE 2.1 (Stephens, Smith, & Donnelly, 2001), following McCracken, Barger, Bulgarella, Johnson, Kuhner, et al. (2009). All gametic phases ( $n = 187$  individuals) were identified with 100% posterior probability. Because we did not find much variation among individuals, we did not reconstruct a rooted gene tree using the haemoglobin data; instead, we evaluated the geographic distribution and abundance of haplotypes using a median-joining haplotype network. To determine whether

variation in DNA sequences resulted in non-synonymous amino acid changes in the secondary structure of the haemoglobin protein, we eliminated introns and translated haplotype sequences.

### 2.4 | Population demography statistics in HBA2 and mtDNA allele frequencies

We calculated summary statistics (gene diversity, nucleotide diversity) and searched for evidence of natural selection or population size changes (Tajima's  $D$ , Fu's  $F$ ) in DNAsp 5.10.1 (Librado & Rozas, 2009), and estimated pairwise genetic differentiation calculating  $\Phi_{ST}$  and its statistical significance with 10,000 permutations in Arlequin 3.5 (Excoffier & Lischer, 2010) separately for the haemoglobin and control region genes. These estimates were calculated for comparisons between three main populations (defined based on groups recovered by the mtDNA; see below), and also between rivers within the Central (Pachachaca and Chillón) and Southern (Malargüe and Arroyo Grande) Andes subpopulations.

### 2.5 | Morphometric analyses

Eight morphological measurements previously described by Gutiérrez-Pinto et al. (2014) were collected from each adult, non-moulting duck in the field: body mass ( $\pm 1$  g), skull length (occipital condyle to beak tip;  $\pm 0.1$  mm), wing chord (carpal joint to longest primary feather unflattened;  $\pm 0.1$  mm), tarsal bone length (inner bend of the tibiotarsal articulation to base of the toes,  $\pm 0.1$  mm), tarsal full length (ankle joint to toe joint,  $\pm 0.1$  mm), beak height and width at nares ( $\pm 0.1$  mm), culmen length from nares (distal edge of nares to beak tip,  $\pm 0.1$  mm) and total culmen length ( $\pm 0.1$  mm). All variables were normally distributed and homoscedastic as indicated by Shapiro–Wilk and O'Brien tests, respectively.

To determine whether morphometric data can diagnose distinct phenotypic groups, we conducted two types of analyses. First, we assigned specimens to the groups recovered by the mtDNA analysis (see below) and asked whether such groups can be distinguished in multivariate morphometric space by performing a Linear Discriminant Analysis (LDA) using the MASS package (Oksanen et al., 2015) for R version 2.15.1 (R Core Team, 2016). We used the raw data, evaluated separately for males and females. In addition, we assessed whether morphological groups were separated by gaps in multivariate space using the gaps in continuous characters across geography method (GCG, Zapata & Jiménez, 2012). This method quantitatively evaluates whether there are discontinuities between populations in the distribution of their evaluated morphological variables, and tests whether patterns can be explained by geographic variation within a population. For this analysis, we ran a principal components analysis (PCA) and used the default options to test for gaps

in multivariate space using all eight PC axes (overlap threshold = 0.10 and statistical confidence = 0.90). Second, we did not assign specimens to groups a priori and instead estimated the number of distinct normal distributions that best fit the pooled morphological data using normal mixture models following procedures and R code described by Cadena, Zapata, and Jiménez (2018). For this analysis, we used the same multivariate space defined above and examined support for models specifying the existence of one to seven morphological groups. We set the upper limit to seven morphological groups because that is the number of “species” of *Merganetta* originally described based on morphology (Callaghan, 1997).

### 3 | RESULTS

#### 3.1 | Phylogeography

All of our genetic analyses point to the existence of three Torrent Duck lineages showing little within-population mtDNA genetic variation and experiencing no (or very low) gene flow among them. The maximum-likelihood tree estimated by RAxML using control region sequences (Figure 2c) recovered three distinct clades seemingly matching current subspecies taxonomy: (a) a Northern Andes clade, including individuals from Colombia, Ecuador and northern Peru (Cajamarca and San Martín); (b) a Central Andes clade, comprising individuals from Peru (Lima, Apurímac and Ayacucho) and north-western Bolivia (La Paz); and (c) a Southern Andes clade with individuals from south-eastern Bolivia (Santa Cruz) and Argentina. Relationships among the three groups were unresolved: in the maximum-likelihood analysis, we found low (<65%) bootstrap support for the branch suggesting a closer relationship between the Northern and Central Andes clades (Figure 2c), whereas the Bayesian analysis did not find strong support for any particular branching pattern, recovering a basal polytomy (tree not shown, see clade posterior probabilities in Figure 2c). Mean uncorrected genetic distance between the three clades was 5.5% (Northern vs. Central Andes: 5.9%; Central vs. Southern Andes: 5.1%; Northern vs. Southern Andes: 5.5%); the similar divergence between lineages can be considered a signature of rapid divergence.

The profound geographic subdivision in the mtDNA was also recovered by the haplotype network (Figure 3a), which further revealed that different rivers within main clades share some haplotypes. Despite haplotype sharing, we found high  $\Phi_{ST}$  values between rivers (Table 1), suggesting significant population genetic structure among rivers within major geographic regions. Estimates of haplotype and nucleotide diversity were very similar in different lineages (i.e., geographic regions) and subpopulations (i.e., rivers within regions), but were remarkably low in the Northern Andes, being an order of magnitude lower than in any other region despite comparable sample sizes (Table 2). We found no evidence of selection or of changes in population size: Tajima's D and Fu's *F* statistics were not significant in any lineage (Table 2).

We found little variation in the HBA2 gene, with only five haplotypes in our entire range-wide sample. The star-like shape of the haplotype network (Figure 3b) revealed a presumably ancestral haplotype present in all populations and at least one private haplotype for each main clade recovered using the mtDNA data. Although geographic variation in haemoglobin genes has been previously documented (Lozano-Jaramillo et al., 2018), the presence of private alleles is interesting in a gene often subject to intense natural selection and supports a long history of isolation among lineages. Most of the haemoglobin polymorphisms were located at introns and one non-synonymous substitution was found, corresponding to the previously described Ala/Thr- $\alpha$ 77 substitution (McCracken, Barger, Bulgarella, Johnson, Sonsthagen, et al., 2009); this substitution appears to occur only in the Central Andes (Figures 2c and 3b) and was not sampled at high elevation or moderately high elevation in the Argentine or Colombian populations, respectively.

#### 3.2 | Morphology

All analyses showed that the three Torrent Duck lineages may be distinguished using morphological measurements at some level. First, although there is overlap between groups, the LDA results show that at least 50% of all the individuals within a given lineage can be distinguished from individuals in other lineages based on the measurements analysed

**TABLE 1** Pairwise  $\Phi_{ST}$  values among populations of Torrent Ducks from different rivers

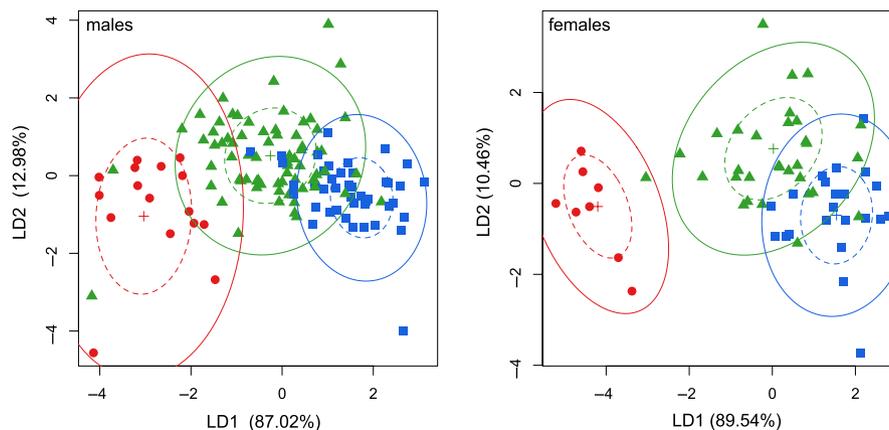
$\Phi_{ST}$	Quindío	Apurimac	Chillón	Marlarije	A. Grande
Quindío		0.8472***	0.67027***	0.72747***	0.86469***
Apurimac	0.85374***		0.06048***	0.86779***	0.91872***
Chillón	0.92311***	0.38939***		0.77711***	0.84605***
Marlarije	0.99337***	0.79524***	0.88945***		0.03822
A. Grande	0.96453***	0.80195***	0.88439***	0.26814***	

Note: Above diagonal:  $\Phi_{ST}$  values for the HBA2 gene; below diagonal:  $\Phi_{ST}$  values for the mtDNA control region. Significant differentiation marked with asterisks (\*\*\*)  $p < 0.000$ .

**TABLE 2** Summary statistics describing the genetic diversity and demographic changes in populations of Torrent Ducks from different rivers

Population	<i>N</i>	<i>h</i>	var	<i>Hd</i> ± <i>SD</i>	$\pi$ ± <i>SD</i>	Tajima's <i>D</i>	Fu's <i>F</i>
mtDNA							
Quindío	24	2	2	0.083 ± 0.075	0.00026 ± 0.00023	−1.51	−0.192
Peru	108	17	30	0.845 ± 0.024	0.01281 ± 0.00041	1.21473	2.584
Apurimac	51	11	24	0.868 ± 0.023	0.01136 ± 0.00102	1.08197	3.097
Chillón	57	7	21	0.547 ± 0.062	0.00758 ± 0.00089	0.12896	4.715
Argentina	50	11	10	0.840 ± 0.029	0.00296 ± 0.00041	−0.50171	−3.198
Malargüe	17	4	3	0.419 ± 0.141	0.00073 ± 0.00028	−1.37718	−1.936
A. Grande	33	8	10	0.801 ± 0.046	0.00333 ± 0.00061	−0.49353	−0.987
Overall	198	40	94	0.929 ± 0.009	0.03552 ± 0.00110	1.11711	4.149
HbA							
Quindío	44	2	1	0.130 ± 0,066	0.00034 ± 0.00017	−0.60	−0.304
Peru	206	2	1	0.277 ± 0,035	0.00073 ± 0.00009	0.63905	1.348
Apurimac	92	2	1	0.161 ± 0,049	0.00042 ± 0.00013	−0.21262	0.2
Chillón	114	2	1	0.355 ± 0,043	0.00094 ± 0.00011	0.98984	1.616
Argentina	122	3	2	0.195 ± 0,046	0.00059 ± 0.00015	−0.58754	−0.777
Malargüe	40	3	2	0.309 ± 0,087	0.00104 ± 0.00032	−0.30763	−0.231
A. Grande	82	2	1	0.137 ± 0,049	0.00036 ± 0.00013	−0.37823	−0.049
Overall	374	5	4	0.650 ± 0,011	0.00248 ± 0.00005	0.86155	1.264

Note: This table shows total number of individuals (*N*), number of haplotypes (*h*), number of variable sites (var), gene diversity (*Hd*), nucleotide diversity ( $\pi$ ), Tajima's *D* and Fu's *F* per population. Note that all Tajima's *D* and Fu's *F* are not significant.



**FIGURE 4** Morphological variation in Torrent Duck geographic groups as summarized by the Linear Discriminant Analyses (LDA). Percentages beside axis names depict the amount of variance explained by them. Red dots, green triangles and blue squares identify the Northern, Central and Southern Andes clades, respectively. Outer solid-line ellipses delimit the area enclosing 90% of the individual points in each group, whereas inner broken-line ellipses encompass 50% of those points. Coloured crosses mark group centroids

(Figure 4; note that broken-line ellipses do not overlap for males or females). The differences are confirmed by relatively low error rates (13.0% for males and 14.8% for females) in the classification of individuals in the three groups based on the predicted morphometric values from the LDA (Table 3). It appears that most differences among lineages are related to bill dimensions: in males, the components with the highest loadings in LDA were bill width and length for

axis 1, and bill height and length, and tarsus size for axis 2 (Table 4). Similarly, in females variables loading more strongly on axis 1 were bill width, skull length and tarsus size, and bill width and length, and skull length on axis 2 (Table 4). The analysis of spatial eigenvectors implemented in the GCG method did not reject the hypothesis that variation in morphology could solely be explained by within-species geographic variation (Table S4). However, even though

**TABLE 3** Confusion matrix from the linear discriminant analysis illustrated in Figure 3, showing the number of individuals correctly and incorrectly identified by the analysis as belonging to any of the lineages evaluated based on the morphometric measurements

	Predicted		
	Northern Andes	Central Andes	Southern Andes
Actual			
Males			
Northern Andes	14	2	0
Central Andes	2	65	9
Southern Andes	0	4	35
Females			
Northern Andes	8	1	0
Central Andes	0	25	3
Southern Andes	0	5	19

there are no morphological discontinuities among geographically adjacent lineages (i.e., Northern vs. Central Andes and Central vs. Southern Andes; Figure S2), this method did detect a gap separating the morphological space occupied by the Northern and Southern Andes groups, for both males and females (Figure S2e,f).

The normal mixtures analysis, which used no a priori information about groups, provided maximum support for models specifying two or three morphological groups (i.e., 2 or 3 distinct phenotypic distributions) in both males and females (Table 5). Close examination of the results revealed that no individuals from the Northern Andes were assigned to the same phenotypic group as individuals from the Southern Andes in any model, confirming the distinctiveness of individuals from these two regions (Table 3 and Figure 5). Likewise, nearly all individuals from the Northern Andes clade were consistently assigned to a group separate from those of the Central Andes clade both in the model specifying two phenotypic groups and in the model specifying three groups; however, up to 7% of the males and 3% of the females from the Central Andes were assigned to phenotypic groups where most of the individuals from the Northern Andes were included, suggesting that evidence for distinct morphometric differences between these two regions was incomplete. Differences between the Central and Southern Andes were much less obvious; in models specifying both two and three morphological groups, individuals from these two regions were not consistently assigned to exclusive groups (Figure 5).

Taken together, the above results point to the existence of at least two phenotypic groups defined by morphological variation in the sample of Torrent Duck populations we examined. The Northern Andes group is the most distinct of the three.

**TABLE 4** Variable loadings for the linear discriminant analysis (LDA) axes, and means for each morphological character in each of the geographic groups identified in the mtDNA analysis

Measurement	Males			Females				
	LD1	LD2	Group means (Males)	LD1	LD2	Group means (Females)		
			Northern	Central	Southern	Northern	Central	Southern
Body mass (g)	0.0215	-0.0110	393.8 ± 22.3	445 ± 43.1	504.4 ± 42.3	0.0218	0.0119	405.5 ± 27.9
Wing chord (mm)	0.0508	0.0376	148.8 ± 4.5	170.7 ± 8.9	180.3 ± 4.1	0.1262	0.0163	162.8 ± 4.8
Tarsal bone length (mm)	0.0682	0.2272	39.8 ± 1.7	40.6 ± 1.7	40.9 ± 3.9	0.0104	0.1373	39.1 ± 1.4
Tarsal full length (mm)	-0.0265	-0.2775	49 ± 1.3	48.9 ± 1.7	50.1 ± 2	-0.1687	-0.1992	47.3 ± 1.6
Total culmen length (mm)	-0.1568	-0.1452	29.1 ± 1.1	28.5 ± 1.5	29.2 ± 1.8	-0.0927	-0.1335	27.1 ± 1.3
Culmen length from nares (mm)	-0.0877	-0.3435	21 ± 2.7	20 ± 1.3	20.8 ± 1.4	0.0886	-0.2314	20 ± 4.6
Beak height (mm)	-0.0041	0.4348	9.4 ± 0.8	10.1 ± 1	9.9 ± 0.6	-0.0332	-0.2245	9.2 ± 0.8
Beak width (mm)	-0.4217	0.0039	11.7 ± 1.5	11.6 ± 0.6	11.3 ± 1.1	-0.4713	1.0080	10.6 ± 0.6
Skull length (mm)	0.0378	0.0787	72.6 ± 1.6	73.5 ± 2.1	75.2 ± 2.2	0.2217	-0.5015	70.6 ± 1

**TABLE 5** Bayesian Information Criterion (BIC) support for each of seven evaluated group divisions, for males and females.  $\Delta$ BIC was calculated by subtracting each model's value from the best model's value

No. of groups	Males		Females	
	BIC	$\Delta$ BIC	BIC	$\Delta$ BIC
1	-5722.18	215.83	-2555.73	87.66
2	-5509.54	<b>3.19</b>	-2468.07	<b>0.00</b>
3	-5506.35	<b>0.00</b>	-2496.61	28.55
4	-5526.61	20.26	-2539.10	71.03
5	-5543.25	36.90	-2574.60	106.53
6	-5576.73	70.38	-2573.80	105.74
7	-5598.85	92.50	-2620.85	152.78

Bold indicates BIC support for the two best models.

## 4 | DISCUSSION

### 4.1 | Geographic variation in Torrent Ducks and diversification in the Andes

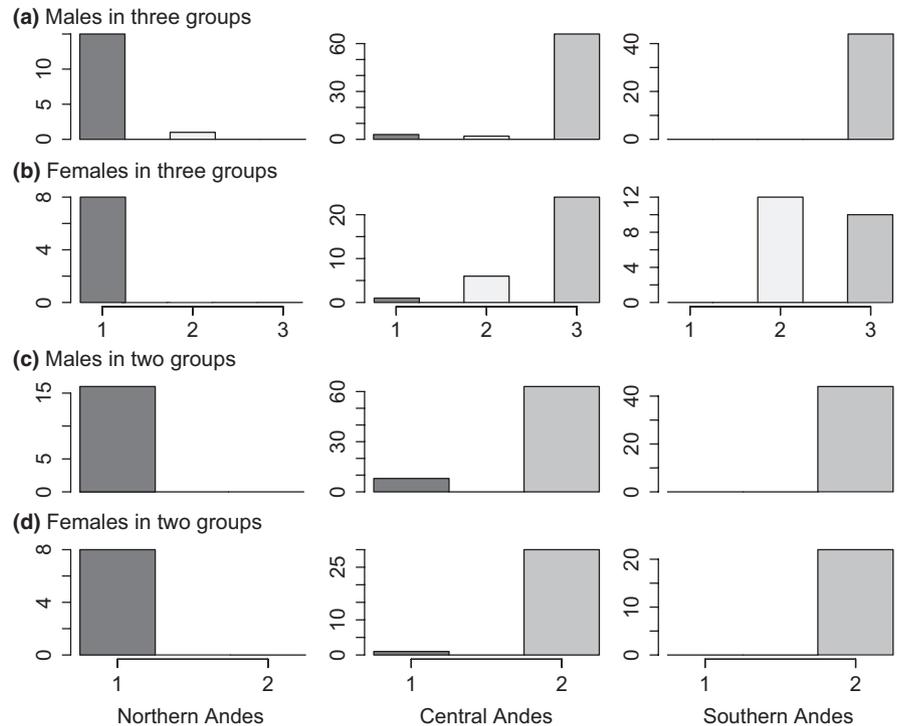
Analyses of geographic variation in Andean birds have yielded rich insights about population differentiation and speciation. In particular, classic studies of plumage and morphometric variation were instrumental in establishing a putative role for barriers in the landscape as well as changes in climate and topography in space and time as drivers of diversification (Chapman, 1917; Graves, 1988; Remsen, 1984; Vuilleumier, 1969). Classic ideas about barriers and climate influencing population divergence have been confirmed by a variety of more recent studies examining patterns of genetic differentiation and evolutionary relationships of birds from Andean cloud forests (Cadena, 2007; Chaves & Smith, 2011, Parra, Remsen, Alvarez-Rebolledo, & Mcguire, 2009; Prieto-Torres, Cuervo, & Bonaccorso, 2018; Quintero, Ribas, & Cracraft, 2013; Rheindt, Cuervo, & Brumfield, 2013; Ribas, Moyle, Miyaki, Cracraft, 2007; Sedano & Burns, 2010; Van Doren et al., 2018; Weir et al., 2008; Winger et al., 2015, Winger, 2017; see additional references in Avendaño, Arbeláez-Cortés, & Cadena, 2017). The increasing integration of molecular data sets with data describing geographic variation in plumage, morphometrics, ecology and physiology has further advanced studies of avian speciation in the Andes, enabling a more complete understanding of patterns and processes involved in diversification (Benham & Witt, 2016; Lozano-Jaramillo et al., 2018; Milá, Wayne, Fitze, & Smith, 2009; Natarajan et al., 2015; Seeholzer & Brumfield, 2018; Winger & Bates, 2015). Nonetheless, to fully understand how historical and evolutionary processes have influenced species histories to result in contemporary patterns of avian diversity in the Andes, one needs studies of differentiation across species with varying habitat preferences and life

histories. To date, however, much of what we know about the phylogeography of Andean birds is based on analyses of cloud forest species, especially in small-bodied groups (notably passerines and hummingbirds). Prior to this study, no phylogeographic analysis had focused on Andean birds sharing latitudinal and elevational distributions with cloud forest birds yet differing in habitat preferences due to their association with riverine/aquatic environments. Although there are several studies on the phylogeography of Neotropical waterfowl species (Bulgarella et al., 2012; Lozano-Jaramillo et al., 2018; McCracken, Bulgarella, et al., 2009; Muñoz-Fuentes, Cortázar-Chinarro, Lozano-Jaramillo, & McCracken, 2013; Wilson, Peters, McCracken 2013), none of them focused on species associated with rivers on forested slopes. Furthermore, ours is the first analysis of Andean waterfowl species considering variation in mitochondrial and nuclear genes across the range of a widespread species in the light of quantitative estimates of morphological differentiation among populations.

Using information from the mtDNA control region, the HBA2 gene and morphological measurements, we found a deep subdivision among Torrent Duck lineages from the northern, central and southern portions of the Andes. Although there is considerable variability in the evolutionary rate of the control region (Ruokonen & Kvist, 2002), assuming a rate of sequence divergence of 9.7% per million years ( $4.8 \times 10^{-8}$  s/s per year), about 4.6 times faster than mtDNA coding regions (Peters, Gretes, & Omland, 2005), would indicate that divergence among Torrent Duck groups occurred roughly 567,000 years ago. These groups, which remain distinct despite some potential for geographic overlap (Figure 1c–e), partially coincide with long noticed morphological variation among Torrent Duck populations that led to the recognition of at least three subspecies based mainly on differences in size and in the overall coloration pattern of males (Carboneras, 1992; Figure 2c and Figure S1). The Northern Andes lineage encompasses all the known range of the *colombiana* form (Figure 1a), but also includes samples from northern Peru slightly south of the North Peruvian Low. Similarly, the Southern Andes lineage extends over the full range of the *armata* form (Figure 1a), but contains samples from as far north as central Bolivia referable to the *leucogenis* form.

The distribution limits of Torrent Duck subspecies partially coincide with those of numerous waterbird species along the Andes, which led to the identification of three major geographic regions (Páramo, Puna and Southern Andes) in an analysis of the evolution of the avifauna of Andean wetlands (Fjeldsá, 1985). The main geographic limits of those regions are the North Peruvian Low (NPL) and the Bolivian Altiplano, both associated with habitat transitions (Fjeldsá, 1985; Vuilleumier, 1969). Several phylogeographic studies of Andean birds have also identified both the NPL and the Bolivian Altiplano as areas associated with genetic structure

**FIGURE 5** Number of specimens assigned to each of the morphological groups determined by the normal mixture analysis. This figure illustrates the individual assignment in three groups for males (a), three groups for females (b), two groups for males (c) and two groups for females (d). Note that the analysis considers, for the most part, the Northern Andes group as a different entity from both the Central and Southern Andes groups



in forest birds with similar distributions along the Andes (e.g., NPL: Benham, Cuervo, McGuire, & Witt, 2015; Cadena et al., 2007; Gutiérrez-Pinto et al., 2012; Winger et al., 2015; Bolivian Altiplano: Álvarez-Varas, González-Acuña, & Vianna, 2015; Bukowski et al., 2017; Loughheed et al., 2013). Genetic breaks suggesting the existence of barriers to gene flow in Torrent Ducks partially coincide with those areas. On the one hand, it is difficult to determine whether the NPL truly constitutes an effective barrier between Torrent Duck lineages. Our only sample immediately south of the NPL grouped with the Northern Andes lineage (Figure 2a,c), suggesting that a barrier to gene flow might actually be located south of the NPL. However, our sparse sampling around the area does not allow us to discard the possibility of ongoing but limited gene flow across the NPL, where there is some potential for ecological continuity (Figure 1c,d). In addition, the NPL region is topographically complex and consists of various potential watersheds where Torrent Ducks may have existed at various moments in the past, implying that barriers to dispersal for this species may not precisely coincide in space with barriers for cloud forest species. The complexity of the NPL region has further resulted in not all species having breaks or limits mapping to the same areas (Parker, Schulenberg, Graves, & Braun, 1985). Therefore, intensive sampling on both sides of the NPL and surrounding areas in La Libertad, Ancash and Huanuco is needed to clarify the limits between Torrent Duck lineages from the Northern and Central Andes. On the other hand, the Bolivian Altiplano seems to be an effective barrier separating the lineages from the Central and Southern Andes; more specifically, the high

elevations of the Tunari mountain range (Cochabamba province) seem to produce a distribution gap where Torrent Ducks have not been recorded (Figure 1b).

The observed pattern of relatively rapid divergence among well-differentiated groups, which does not allow to clearly disentangle their relationships, has also been recovered in several codistributed species occupying forest habitats (Cadena, 2007; Cadena et al., 2007, 2019; Chaves & Smith, 2011; Gutiérrez-Pinto et al., 2012; Isler, Cuervo, Bravo, & Brumfield, 2012; Pérez-Emán, 2005; Weir et al., 2008). The presence of such seemingly common patterns in phylogeographic studies of Andean birds suggests that bird assemblages, including species occupying different habitats, may have been affected by features of the landscape and climatic or tectonic changes in similar ways. The extent to which assemblages responded in concert to common biogeographical events, however, must be examined in analyses considering genealogical patterns and estimates of the timing of population divergence jointly across species (Smith et al., 2014). Comprehensive comparative analyses of the tempo and mode of lineage differentiation across multiple Andean species will be instrumental to understanding the role of various historical and evolutionary processes in the origin and maintenance of the high diversity of birds in the region.

#### 4.2 | Distinct lineages of Torrent Ducks: Evidence for more than one species?

Our analysis of morphological variation found differences among lineages identified in the mtDNA analysis in mensural

traits (Figures 4 and 5, Tables 4 and 5, and Figures S2 and S4). A possible explanation for the lack of significance in the analysis of spatial eigenvectors (Table S4) is that the pattern of morphological variation in our study system is simple and can be described with a simple linear regression relating latitude and morphology (i.e., isolation by distance; Gutiérrez-Pinto et al., 2014), whereas spatial eigenvectors are powerful in detecting complex geographic patterns in morphology (Zapata & Jiménez, 2012). Still, the evidence points to, at least, a highly differentiated population from the Northern Andes. As stated before, phenotypic differences between Torrent Duck populations have long been recognized (Figure 2b and Figure S1; see Callaghan, 1997 and Carboneras, 1992), and a previous analysis of some morphometric differences within and among the same populations found clear differences in size (Gutiérrez-Pinto et al., 2014). The causes of geographic variation in morphology are unknown and await further study; potential roles for selection related to diet (Torrent Ducks seem to have rather generalist diets, and macroinvertebrate composition does not differ much between Andean rivers; Cerón & Boy, 2014; Cerón, Trejo, & Kun, 2010; Goldsmith, 2006; Naranjo & Avila, 2003; Ramirez, Botero, & Kattan, 2014) or thermoregulation (Symonds & Tattersall, 2010), as well as neutral processes, remain to be tested. However, we assume geographic variation at least partly reflects quantitative genetic variation as opposed to plasticity (Cadena et al., 2018; Fisher, 1918). Persisting phenotypic differences among lineages despite the potential for gene flow (Figure 1c–e) may reflect the existence of migration–selection balance maintaining them as distinct lineages.

The Northern Andes lineage, corresponding to the *colombiana* subspecies, seems to be the most different of the three; it has the smallest body size, shows the least overlap in morphological measurements with the other two lineages (Figures 4 and 5 and Figure S2), exhibits the lowest genetic diversity (Table 2) and the highest genetic structure when compared to either Central or Southern Andes groups (Table 1), and occupies the most stable environments in terms of temperature, precipitation and seasonality. It would be interesting to conduct a more detailed sampling of this group considering the high topographic complexity characteristic of the region it inhabits, within which marked population structure exists in various other organisms (Cadena et al., 2007; Chaves & Smith, 2011; Guarnizo, Amézquita, & Bermingham, 2009; Gutiérrez-Pinto et al., 2012; Pérez-Emán, 2005; Valderrama et al., 2014). The Colombian population is not currently considered under any immediate level of threat (Renjifo, Amaya-Villarreal, Burbano-Girón, & Velázquez-Tibatá, 2016; Renjifo et al., 2013), but it may be of conservation concern because it has low densities compared with some regions of the Central and Southern Andes (Cardona & Kattan, 2010; Naranjo & Avila, 2003; Ramirez et al., 2014; Sardina Aragón, Rivera, & Politi, 2011).

Differences between the Central and Southern Andes lineages (the *leucogenis* and *armata* subspecies, respectively)

are arguably less clear. These two groups can be clearly distinguished genetically (Figure 2c), but their morphologies are more similar (Figures 4 and 5 and Table 3; Figure S2.). Historically, patterns of phenotypic variation in the Andes of southern Peru, Bolivia, and northern Argentina and Chile have not been well understood, leading to the descriptions of three additional subspecies based on subtle morphological differences that are no longer recognized from this area. The apparent existence of a continuum in many of the characteristics defining the lineages of the Central and Southern Andes suggests the possibility that groups that are clearly distinguishable units at the extremes of their ranges vary clinically or hybridize at a contact zone. Observations of Torrent Ducks in the Altiplano area are less common than in the rest of the range (note the gap in Figure 1b), thus making it difficult to evaluate this hypothesis.

## 5 | CONCLUSION

Evidence from genes, plumage and morphology points to the existence of the same set of three distinct populations of Torrent Ducks, which appear to be on separate evolutionary trajectories. The data we have presented revealed that despite their presumably high dispersal abilities allowing them to track dynamic habitats, birds associated with riverine environments may exhibit patterns in population structure similar to those observed in closed forest species with more limited dispersal. This is evidenced by the marked divergence across latitudes in the Andes. Our data may be considered sufficient evidence to treat Torrent Duck lineages heretofore treated as subspecies as separate evolutionary entities and elevate them to species status under some species definitions (De Queiroz, 2007). Their largely allopatric ranges preclude direct assessments of whether these lineages have already attained intrinsic reproductive isolation sufficient to be considered good species under the biological species concept (Mayr, 1942), but their differentiation in phenotype, and mitochondrial and nuclear genes despite potential for hybridization afforded by some environmental continuity at contact zones may reflect evidence of barriers to reproduction (Cadena & Cuervo, 2010). Regardless of the taxonomic status given to these lineages, however, their long history of independent evolution makes them evolutionary significant units worthy of conservation and separate management (Frankham et al., 2012).

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## SUPPORTING INFORMATION

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