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Evidence of genetic structure in a wide-ranging and highly mobile soaring scavenger, the Andean condor

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Abstract

Aim: Evaluating the patterns of genetic variation and population connectivity is fundamental to effectively designing and implementing conservation strategies for threatened species. However, connectivity patterns in highly mobile vertebrates, and especially in avian species, are often overlooked as it is generally assumed to be driven by demographic panmixia or isolation by distance. Herein, we investigated the genetic structure and patterns of connectivity across four biomes in a highly vagile bird, the Andean condor (*Vultur gryphus*).

Location: Four major Neotropical biomes of Argentina (>300,000 km^2): Puna, Monte, Chaco and Patagonia.

Methods: We genotyped 13 polymorphic microsatellite loci plus one sex-determining gene in 300 moulted feathers from 13 roosting sites in the core of species distributional range. We quantified levels of genetic differentiation, population structure, effective gene flow, genetic diversity and assessed sex-biased dispersal events.

Results: We detected genetic structure with a moderate differentiation between the north (Puna and Chaco) and south (Patagonia) regions with a contact zone in the central area (Monte). We observed a spatial pattern of genetic patches with higher levels of gene flow along the Andes range. Although we found no indication of bottlenecks or inbreeding, we observed larger effective population sizes in the south compared to the northern region.

Main conclusions: Our study revealed that, despite the high dispersal potential of condors, demographic panmixia is not consolidated, even in the core of this species range. Our analyses further suggest that gene flow rate is modulated by topographic features, as condors may disperse more following the natural updrafts and lifts along the Andean mountains. Conservation initiatives should prioritize the protection of the Andean corridor to maintain connectivity between the apparent source from Patagonia to the northern biomes.

KEYWORDS
conservation genetics, dispersal, endangered species, gene flow, genetic diversity, vulture

1 | INTRODUCTION

Identifying the forces governing the patterns of genetic differentiation and population connectivity is fundamental to predicting species responses to rapid environmental change (Frankham, 2005; Lande & Shannon, 1996). Such information is particularly consequential for threatened species, where conservation efforts can be enhanced by identifying discrete demographic subpopulations and

understanding how these subpopulations are connected via dispersal (Frankham, 2010; Grauer et al., 2017). However, identifying subpopulations are challenging for highly mobile species that are, at least ostensibly, continuously distributed across the landscape with no obvious barriers (Kozakiewicz, Carver, & Burridge, 2017; Waples & Gaggiotti, 2006). Indeed, a priori expectations for genetic structure in highly vagile species are isolation by distance or demographic panmixia (Waples & Gaggiotti, 2006).

Nonetheless, the vagility and dispersal power of the species can be a misleading trait for predicting structure and levels of connectivity. For example, individual wandering albatrosses (*Diomedea exulans*) can range over 1,000 km, yet exhibit a network of fragmented populations with low genetic diversity due to a high degree of philopatry (Milot, Weimerskirch, & Bernatchez, 2008). Similarly, the European grey wolf (*Canis lupus*) is able to move over distances up to 1,000 km, but presents genetic structure driven by dietary differentiation and habitat preferences (Pilot, Jędrzejewski, Sidorovich, Meier-Augenstein, & Hoelzel, 2012). The Mule deer (*Odocoileus hemionus*), one of the most widely distributed mammals in North America that has a dispersal capacity of 250 km, possesses divergent lineages, which are a product of vicariant events (Latch, Reding, Heffelfinger, Alcalá-Galván, & Rhodes, 2014). These examples illustrate that cryptic genetic patterns can arise from complex and sometimes antagonistic forces, such as food predictability, cost of inbreeding, competition, landscape heterogeneity and more recently anthropogenic causes (Johnson & Gaines, 1990; Northrup, Anderson, & Wittemyer, 2016; Reddy, Cushman, Srivastava, Sarkar, & Shivaji, 2017).

Vultures (Families: Accipitridae and Cathartidae) are exemplar cases of highly vagile vertebrates that presumably exhibit well-connected subpopulations (Crochet, 2000; Le Gouar et al., 2008). These soaring scavengers are specialized in moving efficiently across the landscape by utilizing thermal updrafts to gain altitude and move long distances with little effort (Pennycuick, 1972; Shepard, Lambertucci, Vallmitjana, & Wilson, 2011). They are also a guild of species at risk of extinction; indeed, 16 of 22 vulture species are threatened (Buechley & Şekercioğlu, 2016; Koenig, 2006). The Andean condor (*Vultur gryphus*), the world's largest soaring scavenger (wingspan of 3.2 m and weight up to 16 kg; Ferguson-Lees & Christie, 2001; Alarcón et al., 2017), was historically distributed across the Andes, from the extreme south of Argentina and Chile to the north of Venezuela, including the territories of Colombia, Ecuador, Peru and Bolivia (Houston, 1994), and sprawled into central Brazil (Lambertucci, 2007) and the southern Atlantic coasts of Argentina (Darwin, 1839). Currently, Andean condors are restricted to the Andean Mountains (with the exception of the central mountains of Argentina), where populations have declined significantly over the last century (BirdLife International, 2016). Andean condors are listed as "Near Threatened" by the International Union for Conservation of Nature (IUCN, 2016) and are classified as ¨Critically Endangered¨ in northern South America (Naveda-Rodríguez, Vargas, Kohn, & Zapata-Ríos, 2016). Primary threats to their persistence include poaching, poisoning, collision with electric lines and

reduction in safe and reliable food sources (Lambertucci et al., 2009; Lambertucci et al., 2011; Pauli, Donadio, & Lambertucci, 2018; Wiemeyer et al., 2017). Although precise estimates do not exist, it is speculated that the total number of Andean condors reaches a few thousand individuals, mostly concentrated in Chile and Argentina, with the largest known single population in Patagonia (BirdLife International, 2016; Lambertucci, 2010).

While the remarkable movement capacity of Andean condors has begun to be quantified, with reports of individuals flying 350 km per day and with home range >53,000 km^2 (Lambertucci et al., 2014), little is known whether discrete subpopulations exist and how functionally connected the Patagonian region is with the northern parts of its range. Previous studies performed by sequencing mitochondrial DNA (Hendrickson et al., 2003) and nuclear genes of the major histocompatibility complex (Alcaide, Cadahía, Lambertucci, & Negro, 2010) suggest low genetic variability and high levels of panmixia. However, both studies were relatively limited in sample sizes (38–80 individuals) and the use of genetic markers under possible selection pressures, limiting the detection of fine-scale genetic structure (Toews & Brelsford, 2012). Moreover, female-biased dispersal has been suggested to occur in some vultures (Spiegel et al., 2015), whereby mitochondrial DNA might disperse without a concordant movement of nuclear DNA (Toews & Brelsford, 2012).

Given the lack of accurate information on population structure and connectivity among populations, it is unknown what the current structure and gene flow are across South America in the Andean condor. Such information is particularly critical given recent conservation strategies to reintroduce condors to Venezuela, Colombia, Chile and Argentina, including the initiative to repopulate the Atlantic coast (Astore, Estrada, & Jácome, 2017; Lambertucci, Carrete, Speziale, Hiraldo, & Donázar, 2013). In fact, many of the reintroductions used offspring of individuals from central Argentina to repopulate other areas and even countries such as Venezuela (Astore, 2015; Capdevielle, 2003). This reintroduction strategy could be an effective approach if Andean condors exhibit homogeneous genetic backgrounds and populations are relatively well connected with little local genetic adaptation. On the other hand, such human-assisted reintroductions would be inappropriate if subpopulations are highly divergent due to natural selection (requiring a reassessment of its conservation status in IUCN). In this case, conservation strategies aimed demographic rescue within each subpopulation would be a better alternative and preserve possible evolutionary components of the species (Crandall, Bininda-Emonds, Mace, & Wayne, 2000).

Herein, we carried out an extensive survey of almost half of the Andean condor's distributional range in Argentina across different bioclimatic conditions using noninvasive sampling. We tested the hypothesis of demographic panmixia across the Puna, Monte, Chaco and Patagonia regions and developed a suite of microsatellite markers to assess gene flow across the Andes range and the isolated mountains of central Argentina. Our study area allowed us to assess the patterns and processes of genetic cohesion in the geographic intersection between the largest and apparently viable southern population (potential reservoirs of genetic variability) with the smaller, recovering populations

to the north. We assessed possible genetic signals of isolation by distance and sex-biased dispersal events that might account for genetic dissimilarities in this potentially highly vagile species. Also, because we predicted that the persistent decline of the population during the last century promoted high levels of genetic drift, we investigated possible bottlenecks, estimated effective populations sizes and levels of genetic diversity.

2 | METHODS

2.1 | Study area and sampling

Our sampling of condors spanned >1,300 km latitudinally and approximately 500 km longitudinally (> 300,000 km^2) and encompassed four major Neotropical biomes across Argentina (Cabrera, 1976): (a) Puna, characterized by high elevational plateaus; (b) Monte, featuring large plains interrupted by piedmonts and mountain slopes; (c) Chaco, primarily the central mountains with large open valleys, steep slopes and canyons; and (d) Patagonia, consisting of the Andean forest and the Southern Steppe, including the

forest–steppe ecotone. While little is known about condors in the Puna (Perrig, Donadio, Middleton, & Pauli, 2017), communal roosts and nesting sites have been documented in the Monte region and in the central mountains of Chaco, whereas Patagonia harbours the largest number of roosting sites and is assumed to host the largest population of the species (Lambertucci, 2007, 2010). Within these regions, we collected feathers from 13 communal roosts and foraging sites between 2009 and 2014 (Figure 1). From our collection, we selected 300 samples based on feather condition (i.e., recently moulted and undamaged).

2.2 | Microsatellite analysis

We extracted DNA from noninvasively collected samples by removing the blood clot at the superior umbilicus of each feather shaft (Horváth, Martínez-Cruz, Negro, Kalmár, & Godoy, 2005). We performed genomic isolation with QIAamp DNA Micro Kit (Qiagen, Valencia, CA, USA) in a pre-PCR cleanroom facility at Wisconsin University dedicated to low template DNA and included negative controls in each extraction batch (~10 samples/batch). To ensure the
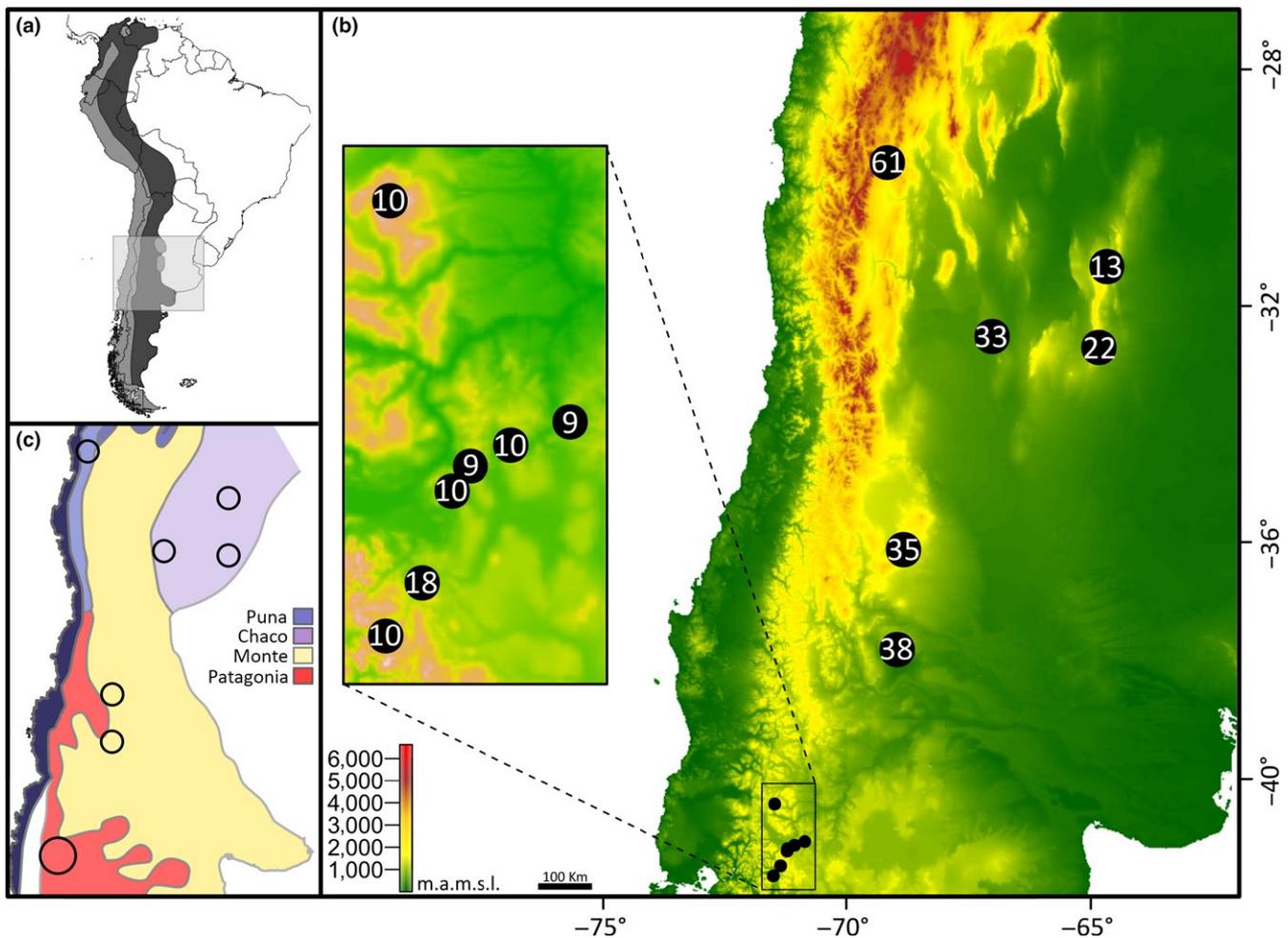

FIGURE 1 Map of South America showing historical (black-grey) and contemporary (grey) distribution range of the Andean condor (*Vultur gryphus*), including the study area (a). Topographic map showing geographic locations and number of samples (b). Diagram of four Neotropical biomes of Argentina and sample sites (c)

absence of contamination, each PCR included one extraction control and one negative "no template" blank. Samples were genotyped at 13 polymorphic microsatellite loci specific to the species (Table 1; Supporting Information Table S1). PCR amplicons were analysed on an ABI 3730xl DNA sequencer (Applied Biosystems, Foster City, CA, USA) and scored with GENEMAPPER v5 software (Applied Biosystems). Genotyping error rates were estimated by random regenotyping 20% of the total sample size. Assessment of potential scoring errors, null alleles and possible large allelic dropout was performed in MICRO-CHECKER 2.2.3 (Van Oosterhout, Hutchinson, Wills, & Shipley, 2004). To avoid possible pseudoreplication (i.e., feathers from same individuals), we identified individuals based on their genotype in CERVUS 3.0.7 (Kalinowski, Taper, & Marshall, 2007; Marshall, Slate, Kruuk, & Pemberton, 1998). Deviations from Hardy–Weinberg and linkage equilibrium were evaluated in GENEPOP 4.2 (Rousset, 2008) with subsequent Bonferroni correction. We assessed marker's power to discriminate individuals with genotype accumulation curves in *poppr* package (Kamvar, Tabima, & Grünwald, 2014) in the R software (R Core Team 2017). We also performed the molecular sexing of each sample by PCR amplification of sex chromosome-link CHD gene region using P2 and P8 primers, followed by *Hae*III restriction digestion (Griffiths, Double, Orr, & Dawson, 1998; Reddy, Prakash, & Shivaji, 2007).

2.3 | Analysis of genetic structure

We assessed the extent of genetic differentiation between biomes with pairwise R_{st} comparisons and conducted an analysis of molecular variance (AMOVA) in GENALEX 6. 5 (Peakall & Smouse, 2006) using the stepwise mutation model (9,999 permutations). We performed a discriminant analysis of principal components in the putative subpopulations to assess the minimum spanning tree (square distances) connecting genetic clusters centroids using the R package *adegenet* (Jombart, Devillard, & Balloux, 2010). We then investigated population structure using genetic assignment through a Bayesian clustering analysis to infer the most likely number of homogeneous genetic units (K) using STRUCTURE 2.3.4 (Pritchard, Stephens, & Donnelly, 2000). We executed 20 independent runs for each K = 1–7, assuming correlated allele frequencies, ancestry admixture model and using sampling locations as prior information. Simulations were performed with a burn-in period of 100,000 iterations and 500,000 MCMC repetitions. The selection of the most reliable value of K was based on both the log-likelihood (LK) and ΔK, a measure of second order of rate change with respect to K (Evanno, Regnaut, & Goudet, 2005). The consensus solutions were calculated and clustered in CLUMPAK 1.1 (Kopelman, Mayzel, Jakobsson, Rosenberg, & Mayrose, 2015). We repeated this analysis for the assessment of cryptic genetic structure within each cluster identified. In addition, we used explicit spatial analysis to test for admixture events among individuals from different genetic clusters using BAPS 6.0 (Corander & Marttinen, 2006). The statistical significance of the admixture level was based on 10,000 simulations from posterior allele frequencies, 200 generated reference individuals for each population

with 100 iterations each and retaining admixture coefficients with *p*-values <0.05. Finally, we performed a detection analysis of first-generation migrants in GENECLASS 2.0 (Piry et al., 2004). We employed a Bayesian criterion (Rannala & Mountain,1997) with MCMC resampling (Paetkau, Slade, Burden, & Estoup, 2004). Critical values (α = 0.01) were obtained from 10,000 simulated individuals using the ratio of the likelihood calculated from the population where the individual was sampled over the highest likelihood value among all population samples (L_h/L_{max}; Paetkau et al., 2004).

2.4 | Isolation and dispersal

To evaluate the extent to which genetic structure was affected by geographic distances and sex-biased dispersal events, we used a series of autocorrelational methods. To explore isolation by distance (IBD), we calculated individual-based pairwise genotypic (allele-sharing distance) and linear distance from the sampling sites. Because IBD could be the result of a continuous cline of genetic differentiation, as well as a consequence of distant clusters, we used two different approaches. First, we conducted Mantel tests (10,000 permutations) in combination with a two-dimensional kernel density estimation to explore the scattering pattern (performed in *adegenet* and *mass* R packages; Venables & Ripley, 2002). Second, we calculated autocorrelational coefficients (r) at evenly spaced distant classes at increments of 222 km, to assess the extent of spatial dependence of gene flow and patterns of spatial heterogeneity. In both cases, statistical significance was determined if the 95% CI of the r values (10,000 bootstraps) in the autocorrelograms did not overlap zero (Peakall, Ruibal, & Lindenmayer, 2003; Smouse, Peakall, & Gonzales, 2008).

To explore sex-biased dispersal effects, we generated distance matrices by sex and tested for the overlapping of 95% bootstrap CI about r between sexes (*Ho*: $r_{males} = r_{females}$) for the whole correlogram and at varying distant classes (Banks, Lindenmayer, Ward, & Taylor, 2005; Banks & Peakall, 2012). In addition, we computed the assignment index correction (*AIc*) for each individual (individual logL – mean logL of the population) and compared them between males and females with Mann–Whitney U tests (Mossman & Waser, 1999).

2.5 | Analysis of genetic diversity

We measured the genetic diversity of each cluster in terms of allelic patterns and through the Shannon's Information Index. We assessed genetic signatures of recent population decline in BOTTLENECK 1.2 (Piry, Luikart, & Cornuet, 1999). Heterozygosity excess tests were based on the two-phase mutation model (allowing 30% multistep mutation) and determined by sign and Wilcoxon tests (10,000 replications). The coefficient of inbreeding (F_{IS}) was calculated in FSTAT 2.9.3 (Goudet, 2002). The significance of the tests was assessed using 95% CI generated by 10,000 iterations of bootstrapping over loci. We also estimated the effective population sizes (N_e) by the linkage disequilibrium method (monogamy mating model), excluding rare allele frequencies <0.05, using NeESTIMATOR 2.01 (Do et al., 2014).

TABLE 1 Summary of the thirteen microsatellite loci developed for the Andean condor: number of alleles (N_A), observed heterozygosity (H_O), expected heterozygosity (H_E) and Polymorphic information content (PIC)

Locus	N_A	H_O	H_E	PIC
Vg011*	8	0.48	0.48	0.43
Vg012	4	0.62	0.59	0.50
Vg025	4	0.31	0.35	0.30
Vg01	7	0.71	0.74	0.69
Vg03*	6	0.46	0.47	0.42
Vg021	4	0.68	0.70	0.64
Vg022	2	0.43	0.45	0.35
Vg02	6	0.17	0.18	0.18
Vg05	9	0.72	0.75	0.71
Vg07	15	0.74	0.74	0.71
Vg09	6	0.70	0.74	0.69
Vg015	6	0.72	0.70	0.65
Vg016	4	0.49	0.46	0.42
Mean	6.2	0.55	0.56	0.51

Note. *Locus in linkage disequilibrium with each other.

3 | RESULTS

3.1 | Microsatellite statistics

We genotyped 300 samples at 94.3% of all loci with an error rate of 0.05%, excluding four samples that failed to amplify. We found no evidence of stutter artefacts, large allelic dropouts or null alleles. Microsatellite loci were polymorphic, ranging from 2 to 15 alleles (Table 1), and sufficiently powerful to discriminate 95% of the multilocus genotypes with at least 5 loci and unique individuals with 8 loci (Supporting information Figure S1). From the 296 samples, we detected 18 duplicate individuals all from the same or neighbouring roosting sites, which we excluded from subsequent analyses, so our final number of unique individuals was 278. We did not detect significant deviation from Hardy–Weinberg or linkage equilibrium in any loci, except in Vg011 and Vg03 that were linked ($p < 0.001$ after multiple test correction). We excluded the less informative loci (Vg03) from subsequent analyses (Table 1).

3.2 | Population structure

Genetic differentiation estimated from the global AMOVA showed a moderate but significant structure between biomes ($R_{ST} = 0.038$; $p < 0.001$). Pairwise comparisons among regions were significant in all cases, while the greatest difference was between Chaco and Patagonia, followed by Puna and Patagonia (Table 2). Our discriminant analysis of principal components was largely concordant with these results, showing the largest genetic distance between Chaco and Patagonia, connected through the Puna and Monte (Figure 2).

TABLE 2 Pairwise R_{ST} comparisons between Andean condors (*Vultur gryphus*) sampled in four Neotropical Biomes of Argentina

	Puna	Monte	Chaco	Patagonia
Puna	-			
Monte	0.020	-		
Chaco	0.011	0.037	-	
Patagonia	0.053	0.010	0.091	-

Note. All pairwise tests were significant at $p \leq 0.05$.

Our Bayesian cluster analysis revealed the highest posterior probability with two clusters ($K = 2$), following a north (Puna and Chaco: mean $q^1 = 0.8$) to south (Patagonia: mean $q^2 = 0.9$) trend, with the individuals of central areas (Monte) exhibiting fairly equal membership proportions (mean $q^2 = 0.6$; Figure 3). Subsequent analysis within each cluster showed no substructure within the south (i.e., $K = 1$) but a weak substructure within the north area ($K = 2$). In the north, most condors of the Puna were assigned to one cluster (mean $q = 0.8$), but individuals from the Chaco region were evenly assigned (mean $q = 0.5$; Figure 3). Therefore, we performed the admixture analysis between Puna, Chaco and Patagonia, while Monte was set as an undefined group to be estimated with respect the other clusters (as implemented in BAPS). Our spatially explicit analysis detected consistent clustering results ($K = 2$) with significant admixture in one condor assigned to the Chaco region (1.5%), one assigned to the Puna (1.6%), two assigned to Patagonia (2.6%) and five individuals in the Monte region (6.8%). To avoid a bias in the detection of potential migrants between north and south regions, we excluded individuals from the Monte region as they showed low assignment probabilities ($q^2 = 0.6$). Thus, we tested first-generation migrants between regions with high membership proportions: Chaco, Puna and Patagonia. The analysis identified one condor assigned to the Puna ($L_h/L_{max} = 3.73$) and one condor assigned to the Chaco ($L_h/L_{max} = 3.01$) in Patagonia, while four condors assigned to Patagonia were sampled in the Puna ($L_h/L_{max} < 2.51$ in all cases).

3.3 | Spatial patterns and sex-biased effects

We detected weak but significant linear correlation between genotypic and geographic distances across the study area ($r = 0.09$, $p < 0.001$). We found multiple densities of genetic relatedness with spatial discontinuities, indicating the presence of genetic patches (Figure 4). This pattern of genetic structure was further corroborated by significant spatial heterogeneity across distance classes ($\omega = 73.89$, $p < 0.001$). We also observed positive genetic autocorrelation up to a distance of 1,110 km ($p < 0.05$; Figure 5). Further autocorrelation analyses performed within the north (Puna and Chaco) and southern regions (Monte and Patagonia) failed to detect IBD as a result of clines (Mantel *p-values* > 0.16 in both cases), although spatial heterogeneity was significant in the north area ($\omega = 29.19$, $p < 0.01$).

Our analysis of sex-biased dispersal was consistent for the three statistical tests at both, broad scale (whole area) and fine scale (within regions), showing no significant differences between sexes
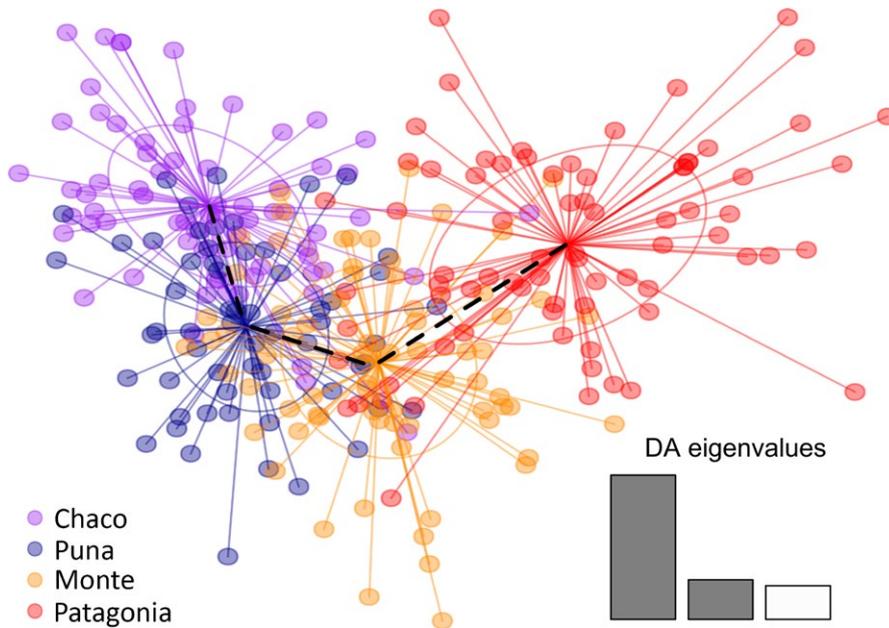
FIGURE 2 Discriminant analysis of principal components for *Vultur gryphus* in Argentina, according to their multilocus genotypes. Sampled bioclimatic regions are indicated with different colours, and individuals are depicted with dots. 95% inertia ellipses and minimum spanning tree (dashed line) are shown
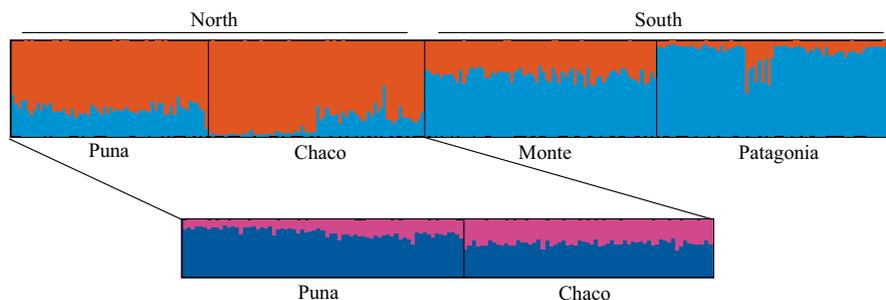

FIGURE 3 Consensus solution of STRUCTURE results, based on the sampling location of *Vultur gryphus* in Argentina (with no prior population information). Vertical bars denote the posterior probabilities of the Bayesian assignment of each individual to each *K* cluster (represented by different colours). Hierarchical structure is shown below the original cluster

at the whole or partial *r* in the correlograms and no evidence of dissimilarities in the *Alc* frequency distributions (*p* > 0.05 in all cases).

3.4 | Genetic Diversity and population demography

The number of alleles per locus, observed heterozygosity, effective number of alleles and average diversity was slightly higher in the southern regions (Patagonia and Monte; Table 3). However, we did not detect differences across biomes or when comparing the north (Puna and Chaco) to the southern regions (Monte and Patagonia; Wilcoxon *p-value* > 0.05 in all cases).

We found no evidence of excess of heterozygosity in any biome or region (Wilcoxon and Sign tests: *p* > 0.10 in all cases), indicating that subpopulations are at mutation-drift equilibrium. In addition, the inbreeding coefficients did not differ from zero in either the north (F_{IS} = 0.013; 95% CI = −0.03–0.05, *p* = 0.35) or the south (F_{IS} = 0.005; 95% CI = −0.03–0.03, *p* = 0.26; Table 3). We also found high effective population size estimated both in the south (N_e = 1276; 95% CI = 470–∞) and, to a lesser degree, in the north (N_e = 383; 95% CI = 208–1234).

4 | DISCUSSION

Despite the tremendous flight capacity of Andean condors, we found that the rate of gene flow was insufficient to create a panmictic and genetically homogenized population in the core of their range. Indeed, we observed moderate levels of genetic differentiation across the four Neotropical biomes sampled, and our analysis of genetic assignment revealed the presence of two major genetic clusters along a north–south trend. Such results are especially striking for this soaring bird that has the potential to move 350 km in a single day (Lambertucci et al., 2014). Nevertheless, our findings are consistent with recent satellite tracking of condors in Patagonia that observed a limited spatial dispersion relative to this species flight potential. While condors possess long daily flights with mean distances of 152 km, they have a relatively small maximum home range of approximately 53,000 km² (Lambertucci et al., 2014). The smaller Griffon vulture (*Gyps fulvus*; 2.6 m wingspan and 7.5 kg; Xirouchakis & Poulakakis, 2008), for instance, only moves an average of 77 km per day in France (Monsarrat et al., 2013) and 18 km per day in Spain, with a maximum home range of
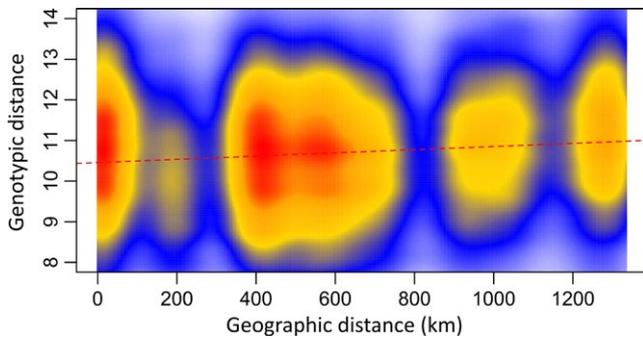
FIGURE 4 Scatter plot of isolation by distance of 278 Andean condors (*Vultur gryphus*) sampled in 13 communal roosting sites across Argentina. The colours represent the two-dimensional kernel density estimation of the correlation between genetic and geographic distances (red, high density; blue, low density; linear trend is shown)

around 57,000 km^2 (García-Ripollés, López-López, & Urios, 2011), and possesses sufficient dispersion to create demographic panmixia across much of Europe (Le Gouar et al., 2008). Additionally, we found no indication of sex-biased dispersal events, as has often been seen as a mito-nuclear genetic discordance in birds (Rheindt & Edwards, 2011; Toews & Brelsford, 2012). Thus, our detection of some structure within condors and discordance with previous studies (Alcaide et al., 2010; Hendrickson et al., 2003) is likely a result of the relative strength of our molecular makers (12 polymorphic microsatellite loci) as well as the spatial (>300,000 km^2) and numerical (*n* = 278) extent of our sampling efforts.

Genetic structure among mobile vultures has been previously found in Old World species, such as the Egyptian vulture (*Neophron percnopterus*; García-Ripollés, López-López, & Urios, 2010), the Cinereous vulture (*Aegypius monachus*; Gavashelishvili,

McGrady, Ghasabian, & Bildstein, 2012) and the Bearded vulture (*Gypaetus barbatus*; Godoy, Negro, Hiraldo, & Donazar, 2004). All three of these species exhibit genetic differentiation and subpopulation structure, although to varying degrees and, apparently by different underlying mechanisms. While the Egyptian vulture exhibits moderate genetic differentiation related to immigration–extinction dynamics between island and continental subpopulations (Agudo, Rico, Hiraldo, & Donázar, 2011), the limited gene flow for the Cinereous vulture seems to be driven by highly philopatric dispersal (Poulakakis et al., 2008), and the strong genetic structure of Bearded vultures has been interpreted as a consequence of historical vicariant events and contemporary admixture (Godoy et al., 2004). Although condors are not separated by oceans, large expanses of plains interrupt the mountainous landscapes, isolating cliffs and mountaintops, favouring a pattern of insular distribution in the Andean avifauna (Nores, 1995). In effect, the spatial pattern of isolated genetic patches in the Andean condor resembles more the island population model of the Egyptian vulture (Agudo et al., 2011).

Our findings suggest that gene flow between the north and south clusters is less than between Patagonia and Chaco regions. This is interesting given that our sample sites between Patagonia and Chaco are geographically closer (1,000–1,200 km) than those of Patagonia and Puna (>1,300 km), but exhibit higher genetic divergence, which was not driven by differences in genetic diversity, as all regions showed similar levels of variability. We believe that a likely explanation for this pattern of structure is a result of the topography separating these areas, as these birds generally optimize energetic expenditures during flight (Shepard et al., 2013). The Puna and Patagonia are connected by the Andes mountain range, which create strong updrafts and a "high-lift" efficient environment for large soaring birds, like condors, to move. In contrast, thermal updrafts

FIGURE 5 Results of spatial autocorrelation in allele frequencies (*r*) of *Vultur gryphus* at increasing geographic distances across central Argentina. 95% confidence intervals (CI) are shown for *r* and zero values (nonoverlapping CIs were considered significantly different)
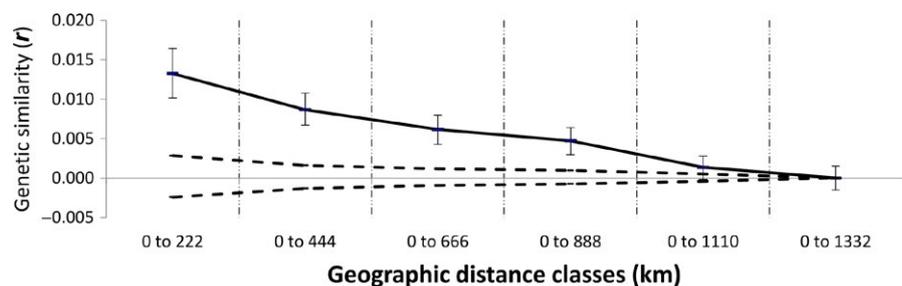

TABLE 3 Summary of number of individuals (*N*); Shannon's Diversity Index (*H*); Mean number of alleles (NA); number of effective alleles (NE); number of private alleles (*P*); average observed heterozygosity (HO); expected heterozygosity (HE); and inbreeding coefficient (FIS) for *Vultur gryphus* sampled in four biomes of Argentina between 2009 and 2014

Population	N	H	NA	NE	P	HO (SD)	HE (SD)	FIS (95% CI)
Chaco	68	4.23	4.83	2.59	0.33	0.55 (0.19)	0.54 (0.18)	−0.02 (−0.07 to 0.02)
Puna	61	4.11	4.75	2.46	0.25	0.55 (0.15)	0.57 (0.15)	0.04 (−0.004 to 0.08)
Monte	73	4.29	5.00	2.62	0.08	0.56 (0.21)	0.55 (0.20)	−0.01 (−0.05 to 0.03)
Patagonia	76	4.33	5.42	2.97	0.50	0.59 (0.21)	0.59 (0.20)	0.01 (−0.02 to 0.05)

in areas with little topographic relief, as the plains surrounding the central mountains of Chaco, are weaker and prone to disruption by wind speed (Shepard & Lambertucci, 2013). Moreover, our finding of extensive admixture in the Monte suggests this region acts as a contact zone for condors coming from the north and especially the south. In addition, we found slight genetic structure nested within the north area between Puna and Chaco regions. Given significant spatial heterogeneity of genetic autocorrelation, the observed fine-scale structure does not appear to be the result of a linear genetic cline between the Puna and the central mountains of Chaco, but rather suggests an irregular gene flow distribution (Smouse et al., 2008). Altogether, these patterns are consistent with an ¨archipelago¨ of isolated mountains used as stepping stones across the central mountains (Nores, 1995). This is not surprising, as vultures require high slopes to soar and updrafts are considered patchy resources for large soaring birds with high wing loading (Shepard et al., 2011, 2013). Thus, our results suggest that topographic features and climatic conditions, such as relief and wind patterns, are likely important mechanisms in the genetic structure for this large soaring scavenger. However, we cannot rule out other possible intervening forces such as some level of philopatric behaviour, ecological factors or anthropogenic causes.

Even though populations of Andean condor have been declining for the past century, we did not detect evidence for genetic bottlenecks or reduced genetic diversity, especially in the northern region, as previously expected. Indeed, the genetic diversity was similar to those of other widely distributed vultures of the genus *Gyps* and *Neophron*, with observed heterozygosity ranging between 0.47–0.68 (Agudo et al., 2011; Arshad et al., 2009; Ishtiaq, Prakash, Green, & Johnson, 2015; Le Gouar et al., 2008). It is possible that large historical population sizes combined with connectivity among regions helped to buffer the genetic consequences of population declines from more recent human persecution. In addition, the long generational time of this species (lifespan up to 65–75 years; Kasielke & Wallace, 1990; Meretsky, Snyder, Beissinger, Clendenen, & Wiley, 2000) could also contribute to the lack of genetic drift and buffer the erosion of genetic diversity (Hailer et al., 2006; Lippe, Dumont, & Bernatchez, 2006). Thus, while we did not detect bottleneck or inbreeding, this does not mean that Andean condor populations are not experiencing demographic declines or reduced viability, especially given this species is extremely slow life history strategy (Wallace & Temple, 1987) and the effects of drift may appear over a longer time-scale. Indeed, we found a larger effective population size in the southern cluster, more than three times larger compared to the northern cluster, corroborating the observation of a declining population towards the north end of the species distribution (BirdLife International, 2016). Our finding of more migrants from the south to the north suggests a directionality of dispersal from a source population in the south to a potential sink population in the north. If true, continued population declines in the Puna (Arnulphi, Lambertucci, & Borghi, 2017) may affect the gene flow from the healthiest subpopulation of Patagonia, along the Andes to the northern regions and the central mountains of Chaco. Therefore, we recommend that conservation efforts prioritize maintaining connectivity along the Andes with Patagonia, as this latter region could be regarded as a compatible reservoir of genetic variability for southern South America. In addition, we encourage that management plans for translocations of individuals take into account our estimates of effective gene flow of ~1,000 km as reference to infer patterns of postrelease dispersal within the boundaries of the target subpopulation.

5 | CONCLUSIONS

Genetic structure studies in highly mobile birds are severely underrepresented due to the general assumption of strong connectivity via dispersal. However, our findings revealed that even a highly vagile species with extreme flight capabilities exhibit fine-scale barriers to gene flow at the core of its distribution. We suggest that genetic structure is modulated by the energy provided by the landscape to disperse. This energy comes from topographic features involved in flight performance, where mountains promote heterogenic dynamics of gene flow. We propose that the inclusion of a geographic context of gene flow in wide-ranging species with high environmental energy requirements will lead to new insights for conservation and management.

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BIOSKETCH

This work is a collaboration between researchers from Argentina and United States working on vertebrate ecology and conservation biology. We are an interdisciplinary group with research efforts focused on the response of natural populations to anthropogenic disturbance. We use a combination of techniques, including satellite tracking, biochemical analysis, stable isotopes, direct observations and genetic markers to investigate general aspects of ecology and conservation of species in diverse ecosystems. Links: https://grinbic.com/; http://labs.russell.wisc.edu/pauli/

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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