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Evidence of the genetic and spatial structure of *Nasua narica* in Central America and northern South America from mitogenomic analysis

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Carnivores are extremely important in ecosystem dynamics. Coatis (Procyonidae) are a group of Neotropical species with highly developed social behavior. One coati species is the Central American or white-nosed coati (*Nasua narica*). This work describes the analysis of two sets of mitochondrial data for a sample of *N. narica* covering most of the geographic distribution range of the species. The first data set analyzed 74 specimens for three mitochondrial loci; the second, 59 specimens for complete mitochondrial genomes. Our phylogenetic analyses revealed six distinct genetic groups of *N. narica* in southern México, Central America, and South America, which, together with three additional groups found in northern México and southern USA in a previous study, resulted in a total of nine genetically distinct groups of *N. narica*. The first genetic group (G1), which began to differentiate 4.1 to 3.2 million years ago, was located on the Pacific coast of Ecuador and northern Colombia. A second genetic group (G6) was detected in northern Colombia, Panama, and southern Costa Rica, being introgressed by mitochondrial DNA from the mountain coati (*Nasuella olivacea*). The third genetic group (G3) was located in Costa Rica, Nicaragua, El Salvador, Honduras, and southern Guatemala. The fourth genetic group (G4) was located in north-central Guatemala and Belize. The fifth genetic group (G5) was distributed in southern México (Chiapas, Tabasco, Campeche, Quintana Roo, and Yucatán) and northern Guatemala. Finally, the sixth genetic group (G2) was found only in Mérida (Yucatán, México). Groups G2 to G5 became mitochondrially diversified over 1.9 to 1.1 million years. All groups showed high mitochondrial genetic diversity, although the South American genetic group (G1) had the highest diversity. The northern genetic groups (G4, G5) had lower genetic diversity, except for the Merida group, which is likely composed of other undetected subgroups. The existence of six (nine, considering another study) well-developed groups in *N. narica* is related to female phylopatry and climatic changes during the Pleistocene. A spatial autocorrelation analysis showed a very high structure, well in line with the south-to-north colonization of the American continent by *N. narica*.

Los carnívoros son extremadamente importantes en la dinámica de los ecosistemas. Los coatíes (Procyonidae) son un grupo de especies neotropicales con un comportamiento social muy desarrollado. Una especie de coatí es el coatí centroamericano o de nariz blanca (*Nasua narica*). Este trabajo describe el análisis de dos conjuntos de datos mitocondriales para una muestra de *N. narica* que cubre la mayor parte del rango de distribución geográfica de la especie. El primer conjunto de datos analizó 74 especímenes para tres loci mitocondriales; el segundo, 59 especímenes para genomas mitocondriales completos. Nuestros análisis filogenéticos revelaron seis grupos genéticos distintos de *N. narica* en el sur de México, América Central y América del Sur, que, junto con tres grupos adicionales encontrados en el norte de México y el sur de EE. UU. en un estudio anterior, dieron como resultado un total de nueve genéticamente distintas grupos de *N. narica*. El primer grupo genético (G1), que comenzó a diferenciarse hace 4,1 a 3,2 millones de años, se ubicó en la costa del Pacífico de Ecuador y el norte de Colombia. Un segundo grupo genético (G6) fue detectado en el norte de Colombia, Panamá y el sur de Costa Rica, siendo introgresado por ADN mitocondrial del coatí de montaña (Nasuella olivacea). El tercer grupo genético (G3) se ubicó en Costa Rica, Nicaragua, El Salvador, Honduras y el sur de Guatemala. El cuarto grupo genético (G4) se ubicó en el centro-norte de Guatemala y Belice. El quinto grupo genético (G5) se distribuyó en el sur de México (Chiapas, Tabasco, Campeche, Quintana Roo y Yucatán) y norte de Guatemala. Finalmente, el sexto grupo genético (G2) se encontró únicamente en Mérida (Yucatán, México). Los grupos G2 a G5 se diversificaron mitocondrialmente durante 1,9 a 1,1 millones de años. Todos los grupos mostraron una alta diversidad genética mitocondrial, aunque el grupo genético sudamericano (G1) presentó la mayor diversidad. Los grupos genéticos del norte (G4, G5) tuvieron menor diversidad genética, excepto el grupo Mérida, que probablemente esté compuesto por otros subgrupos no detectados. La existencia de seis (nueve, considerando otro estudio) grupos bien desarrollados en *N. narica* está relacionada con la filopatría femenina y los cambios climáticos durante el Pleistoceno. Un análisis de autocorrelación espacial mostró una estructura muy alta, en línea con la colonización de sur a norte del continente americano por *N. narica*.

Keywords: Coati; mitochondrial genes; *Nasua* sp.; phylogeography; Pleistocene; population genetics; spatial patterns.

Introduction

Regardless of the time when North and South America became connected in geological times and the physical substrate that was established in Central America (islands, isthmus of Panama, etc.) for the Great American Biotic Exchange (GABI), the orographic, biotic, biogeographical, and climatological complexity of the zone (southern North America, Central America, and northern South America) is of such diversity and magnitude that evolutionary processes in this area, including diversification and speciation, have occurred at a high speed (Marshall 2007; Hardy *et al.* 2013). Therefore, the evolutionary study of the species with a broad distribution range in this geographic area can reveal essential information for understanding the colonization, adaptation, diversification, and speciation processes of migrant organisms between previously separate continents (Webb 2006; Morgan 2008).

A species that meets these characteristics is the white-nosed coati (*Nasua narica* Linnaeus 1766, Order Carnivora, Family Procyonidae) since it has a wide distribution from North America to northern South America (González-Maya *et al.* 2011). The evolutionary and biogeographical history of procionids is controversial from the molecular and paleontological perspectives (Soibelzon and Prevosti 2013; Nigenda-Morales *et al.* 2019; Ruiz-García *et al.* 2019b, 2020a). In fact, procionids are one of the taxonomic groups that can provide surprising insights into how and when GIBA occurred (Koepfli *et al.* 2007; Forasiepi *et al.* 2014).

Nasua narica is distributed from Arizona and New Mexico (USA) through Central America, including the Pacific coast of Colombia, Ecuador, and northern Peru (Emmons 1990; Emmons and Feer 1997; Tirira 2007, 2011). However, Gompper (1995) excluded the Ecuadorian and Peruvian Pacific areas because this author considered that *Nasua nasua* lives there. Although Gompper (1995) excluded *N. narica* from the South American mammal fauna, other authors, such as those previously mentioned, and the results of the present study postulate the existence of *N. narica* in northwestern South America, which is why we used South American specimens of this species.

Nasua narica is a strongly gregarious species that forms social groups including up to 30 females and juveniles per group, while males tend to be solitary and are the only ones to disperse after reaching sexual maturity (Gompper 1997; Gompper *et al.* 1997, 1998). On the other hand, females are strongly philopatric and frequently do not disperse outside the area where they were born (Valenzuela and Ceballos 2000). This species potentially participates in controlling small-sized pests such as rodents and arthropods, besides being a seed disperser and a potential prey for large cats such as jaguar (*Panthera onca*) and puma (*Puma concolor* (Gompper 1995, 1997).

Four subspecies have been recognized according to body size, differences in coat color, and cranial characteristics (Hershkovitz 1951; Hall 1981; Decker 1991; Gompper 1995). These differences may be related to geographic barriers and ecological differences (Hershkovitz 1951). The four subspecies are: 1) *N. n. molaris* (Merriam 1902; Type locality: Manzanillo, Colima, México), distributed from the north of the Trans-Mexican Volcanic Belt to Arizona and New Mexico USA; 2) *N. n. narica* (Linneus 1766; Type locality: "America", restricted to Achotal, Isthmus of Tehuantepec, Veracruz, México), distributed south of the Trans-Mexican Volcanic Belt to south Panama; 3) *N. n. nelsoni* (Merriam 1901; Type locality: Cozumel Island, Quintana Roo, México), distributed exclusively in the type locality; and 4) *N. n. yucatanica* (Allen 1904; Type locality: Chichen Itzá, Yucatán, México), confined to the Yucatán Peninsula. McFadden *et al.* (2008) designated the insular subspecies as a different species (*N. nelsoni*) based on a morphometric analysis.

To date, only two works have analyzed the genetic structure of *N. narica*. The first, by Silva-Caballero *et al.* (2017), used a fragment of 800 base pairs (bp) of the mitochondrial gene (mt) *Cyt-b* and 12 nuclear microsatellites in 60 specimens from five different populations in México (Nayarit, Jalisco, Morelos, Tabasco, and Quintana Roo). Moderate and high levels of genetic diversity were found for both types of molecular markers (mitochondrial: haplotypic diversity, H_d = 0.968; microsatellites: expected heterozygosity, H_E = 0.774). A total of 22 haplotypes were detected in the five areas analyzed, and each of the populations with unique haplotypes, except for three haplotypes shared between the two geographically closest populations (Puerto Morelos, Quintana Roo, and La Venta, Tabasco). Both genetic markers clearly separated the five populations studied and identified a strong genetic structure between them, suggesting isolation by distance.

The second study was conducted by Nigenda-Morales *et al.* (2019) with sequences of three mt genes (*Cyt-b*, *NAD5*, and *16S rRNA*) and 11 nuclear microsatellites in 85 specimens from Arizona and New Mexico (USA), México (Jalisco, Morelos, Yucatán, and Cozumel Island), Belize, Guatemala, Costa Rica, and Panama. They found a strong genetic structure with five distinct Evolutionary Units (EU). The southernmost (Panama) was the most differentiated EU, with genetic distances between 9.9 % and 10.8 % from the other four EU, and which appeared 3.8 million years ago (Ma). A second EU consisted of specimens from Costa Rica, Guatemala, Belize, Cozumel Island, and Yucatán (México). A third EU included specimens from Morelos (central México), while the fourth EU included specimens from Jalisco (western México); finally, the fifth EU comprised specimens from southwest USA. The diversification of this group was calculated to have occurred 1.2 Ma. The genetic flow took place from south to north and from east to west.

The present study used two sets of mitochondrial genes (three loci: *ND5*, *Cyt-b*, and *D-loop*; and complete mitogenomes) analyzed in 74 and 59 specimens, respectively, of *N. narica* sampled in México, Belize, Guatemala, Honduras, El Salvador, Nicaragua, Costa Rica, Panama, Colombia, and Ecuador. We focused on mtDNA to expand the scope

of previous results with a larger number of data (mitogenomes) and samples of specimens from South America that clearly belong to this species because of their external morphology (phenotype). It is also possible to compare our results with those of Nigenda-Morales *et al.* (2019) since the present study included Colombia and Ecuador, whereas the study referred to was limited to northern Mesoamerica.

Mitochondrial DNA genes allow reconstructing phylogenetic relationships to determine recent intra- or interspecific genetic divergence processes, while nuclear genes reveal deeper relationships (Collins and Dubach 2000, 2001; Cortés-Ortiz *et al.* 2003; Ruiz-García *et al.* 2016). In fact, mtDNA has been extremely effective for detecting new groups or taxa that had been left out with other techniques (Krause *et al.* 2010; Derenko *et al.* 2012; Sawyer *et al.* 2015). Mitochondrial genes have high mutation accumulation rates, short coalescence times, absence of introns and recombination, and haploid inheritance (Avise *et al.* 1987). In addition, although they represent a single linked locus, the selection pressure and evolutionary rates are heterogeneous, depending on the genes considered (Nabholz *et al.* 2012). An additional advantage is that the number of mtDNA copies per cell is high, thus making it easier to obtain sequences and mitogenomes from low-quality samples (teeth, hair, skin, etc.; Guschanski *et al.* 2013). However, caution should be exercised with mtDNA because gene trees do not always match species trees (Freeman and Herron 1998). Also, mtDNA only shows the evolution of female lineages, so hybridization events produced by males as vectors of gene flow go unnoticed (Burrell *et al.* 2009).

Therefore, considering that this work covers the broadest distribution range analyzed to date for *N. narica* and that, for the first time, complete mitogenomes are analyzed for this species, the objectives are to 1) determine the number of lineages in *N. narica* throughout its geographic range, and whether the putative morphological subspecies described for *N. narica* match the molecular groups detected; 2) estimate genetic heterogeneity among these groups and the ancestor-descendant relationship between them; 3) determine the relationship of historical geographic, geological, and climatological events to the divergence times found in the genetic groups of *N. narica*; 4) estimate the levels of genetic diversity within them; and 5) determine significant patterns of spatial structure throughout the area analyzed.

Materials and Methods

Sample collection. We analyzed 74 specimens of *N. narica* from México (n = 25), Guatemala (n = 21), Belize (n = 3), Honduras (n = 7), El Salvador (n = 3), Nicaragua (n = 1), Costa Rica (n = 3), Panama (n = 1), Colombia (n = 4), Ecuador (n = 5), and Robinson Crusoe Island (Chile; n = 1, Figure 1 and Supplementary Table 1). Eight specimens of *Nasuella olivacea* from Colombia were used as an external group, as well as 29 specimens of *Nasua nasua* from Colombia (n = 4), Ecuador (n = 5), Perú (n = 11), Bolivia (n = 3), and Brazil (n = 6). For mitogenomes, there were 59 specimens from México (n = 21), Guatemala (n = 14), Belize (n = 3), Honduras (n = 7), El Salvador (n = 3), Nicaragua (n = 1), Costa Rica (n = 3), Panama (n = 1), Colombia (n = 2), Ecuador (n = 3), and Robinson Crusoe Island (Chile) (n = 1). Samples of six specimens of *N. olivacea* from Colombia were used as an external group, as well as 23 specimens of *N. nasua* from Colombia (n = 4), Ecuador (n = 2), Peru (n = 10), Bolivia (n = 3), and Brazil (n = 4).

The samples come from specimens hunted by indigenous communities and road-killed animals in southern México, and Central and South America (fragments of skin, teeth, and hairs with bulbs). Permission to collect biological materials was requested from the authorities of the communities (in addition to the corresponding ministries). During the sampling process, hunters from the local communities were interviewed to determine the exact source of the samples; these were usually collected within 5 to 15 kilometers of the interview site. Samples were gathered over 22 years (1996–2018).

DNA extraction, amplification, and sequencing. DNA extraction from skin and muscle samples was performed using the phenol-chloroform procedure (Sambroock *et al.* 1989). DNA from follicle hairs and teeth was extracted with Chelex 100 resin (Bio-Rad, Hercules, California, USA) using the protocol of Walsh *et al.* (1991), while the DNA from bones was extracted with the DNeasy Blood and Tissue Kit (Qiagen, Hilden, Germany). These procedures were used for all three mitochondrial loci. Three mt loci were amplified: 1) 407 bp of the *Cyt-b* gene (Irwin *et al.* 1991), 2) 1,800 bp of gene *ND5* (Trigo *et al.* 2008), and 3) 306 bp from the *D-loop* region (Hoelzel *et al.* 1994). The total sequenced length was 2,513 bp.

We used the PCR (Polymerase Chain Reaction) in a final volume of 25 µL: 2µL of 1 mM $MgCl_2$ (CorpoGen), 1 µL of 0.2 mM dNTPs (BioLabs), 1 µL of 0.1 mM of each primer, one Taq Polymerase Unit (CorpoGen), 100–200 ng of DNA template (in 2–4 µL of DNA), 2 µL of 10X Buffer, and 14–16 µL of double-distilled H_2O. The PCR temperatures for gene amplification were 95 °C for 5 minutes, followed by 40 cycles at 94 °C for one minute: 52 °C (*Cyt-b*), 55 °C (*ND5*), and 56 °C (*D-loop*) for one minute, 72 °C for one minute, and a final extension at 72 °C for ten minutes. The amplification products, including positive and negative controls, were run on a 2 % agarose gel stained with ethidium bromide and visualized with ultraviolet light on a transilluminator. Both directions were sequenced using BigDye Terminator v3.1 (Applied Biosystems, Inc., Foster City, California, USA), whose products were analyzed on an ABI 3730 sequencer (Applied Biosystems, Inc., Foster City, California, USA). The sequences were assembled and edited with Sequencher 4.7 (Gene Codes, Corp., Ann Arbor, Michigan, USA).

Nucleotide sequences of the mt*ND5* and *Cyt-b* genes were translated into amino acid sequences to exclude the possibility of nuclear mitochondrial DNA segments (Numts; Lopez *et al.* 1994). All amino acid translations performed showed correct start and stop codons, and a total absence

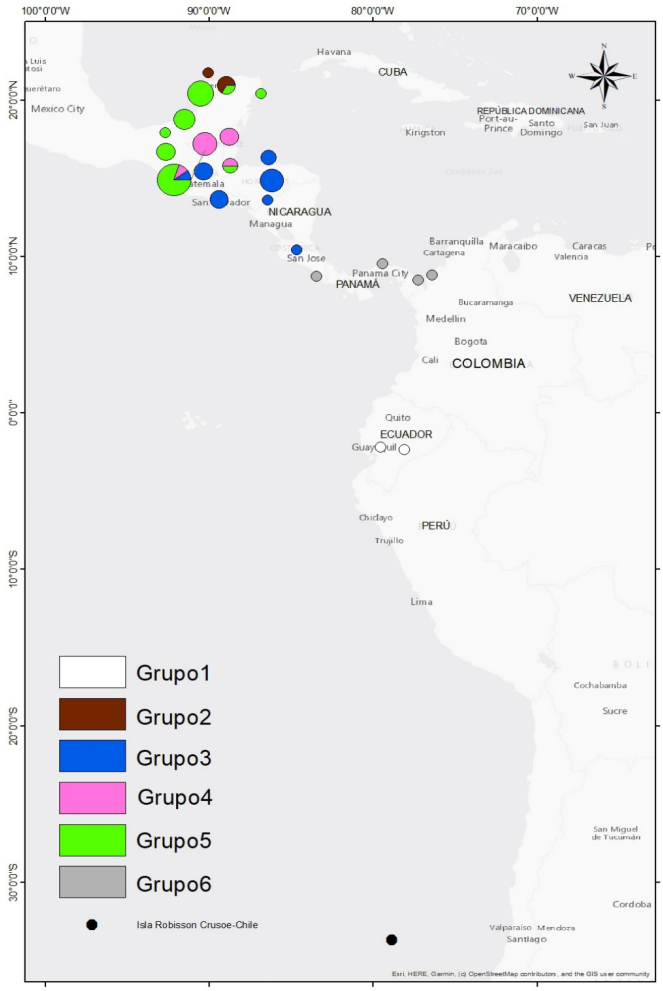

Figure 1. Map of Central America and northern South America where 74 specimens of white-nosed coati (*Nasua narica*) were sampled for three mitochondrial genes (*ND5*, *Cyt-b*, and *D-loop*), 59 of which also sampled for the complete mitogenomes. Circles are proportional to the sample size. The colors of circles mark the different molecular groups detected and are the same colors shown in phylogenetic trees and the haplotype network.

of termination codons. All the mutations observed were synonymous, which is well-related to the absence of Numts in the two mt genes mentioned.

For the mitogenomic analysis, DNA was extracted and isolated from the tissues mentioned above using the QIAamp DNA Micro Kit (Qiagen, Inc. Hilden, Germany) according to the manufacturer's protocol. Mitogenomes were sequenced by "long-template PCR", which minimizes Numts amplification (Thalmann *et al.* 2004; Raaum *et al.* 2005). The PCRs to obtain mitogenomes were performed with the LongRange PCR Kit (Qiagen, Inc. Hilden, Germany), with a reaction volume of 25 µL. The components of each reaction were 2.5 µL of 10x LongRange PCR Buffer, 500 mM of each dNTP, 0.6 mM of each primer, 1 unit of LongRange PCR Enzyme, and 100–250 ng of DNA template. The temperature conditions of the PCRs were 94 °C for 5 min, followed by 45 cycles of 94 °C for 30 s, with an annealing temperature of 50–57 °C (depending on the primer set) for 30 s and an extension of 72 °C for 8 min. Afterward, there were 30 denaturation cycles at 93 °C for 30 s, with annealing temperatures of 45–52 °C (depending on the primer set) for 30 s, and an extension of 72 °C for 5 min, with a final extension of 72 °C for 8 min. Four sets of primers were used to generate overlapping amplicons: PROCYONID1F (ATGAGTAATCAGCCCTTGAT) and PROCYONID1R (ATGCATCCCACGTCAATCAT), approximately 5,000 bp; PROCYONID2F (AAGTAATATGTCTGACATAA) and PROCYONID2R (TCATCTGCATCTATTCTGA), approximately 4,000 bp, PROCYONID3F (CATTTAGAAGCTAATTAAGC) and PROCYONID3R (GTGCAACTCGAAATAAATGT), approximately 4,000 bp; PROCYONID4F (TAATTGTAATAAAGCTATTT) and PROCYONID4R (TGGCACATCTCGATGGAGTA), approximately 3,200 bp. These allowed observing the circularity of the mitochondrial genome (Bensasson *et al.* 2001; Thalmann *et al.* 2004). Both DNA strands were sequenced directly using BigDye Terminator v3.1 (Applied Biosystems, Inc., Foster City, California, USA). The sequencing products were analyzed in an ABI 3730 DNA Analyzer system (Applied Biosystems, Inc., Foster City, California, USA). The sequences were assembled and edited with the Sequencher 4.7 program (Gene Codes, Corp., Ann Arbor, Michigan, USA). The overlapping regions were examined for possible irregularities, such as termination codons. The absence of such irregularities is a valid indication of the absence of Numts. Genes were concatenated (about 16,200 bp) after removing any problematic region with the Gblocks 0.91 program (Talavera and Castresana 2007) under a relaxed approach. Individual alignments were concatenated with SequenceMatrix v1.7.6 (Vaidya *et al.* 2011) to create the final alignment.

The sequences were deposited in the NCBI GenBank under access numbers MT587713-MT587788, MW410859-MW410914, and MW419814-MW419853.

Phylogenetic analyses. The sequences were concatenated for phylogenetic analyses of the three mt loci studied because they showed the same phylogenetic signal. To this end, we used the ILD test ("Incongruence-length difference test"; Farris *et al.* 1995) in the mILD program (Planet and Sarkar 2005). The programs jModeltest v2.0 (Darriba *et al.* 2012) and MEGA 6.05 (Tamura *et al.* 2013) were applied to determine the best nucleotide substitution model, using the Akaike information criterion (AIC; Akaike 1974) and the Bayesian information criterion (BIC; Schwarz 1978).

A Maximum Likelihood (ML) analysis was performed as phylogenetic inference using the RAxML v.7.2.6 program (Stamatakis 2006) with the partition scheme selected by the PartitionFinder 2.0 program (Lanfear *et al.* 2012). This program was used to simultaneously determine the optimal model for nucleotide substitution (which coincided with that of jMoldeltest v2.0) and sequence partition scheme. For partitions, codons 1 + 2, and codon 3 were combined for each gene (for both *Cyt-b* and *ND5* in the case of the data set with three loci and for each of the coding genes in the mitogenomic case. Additionally, RNA genes were included in the mitogenomic analysis and the control region for both data sets). The best-fit models were selected using BIC under a 'greedy' search scheme with a subset of models specific to RAxML. The GTR + G + I model

(Tavaré 1986) was used for the ML tree search, as discussed in the *Results* section. The support for nodes was estimated using the "rapid-bootstrapping" algorithm with 1,000 non-parametric bootstrap replicates (Stamatakis *et al.* 2008). Clades were considered to have good nodal support when bootstrap values were greater than 70 % (loose limit; Hillis and Bull 1993).

The relationships between the haplotypes found were determined using the Median Joining Network algorithm (MJN; Bandelt *et al.* 1999) of the Network 4.6 program (Fluxus Technology Ltd). One advantage of MJN over phylogenetic trees is that it explicitly allows the coexistence of ancestral and descendant haplotypes, while phylogenetic trees treat all sequences as terminal taxa (Posada and Crandall 2001). This allows identifying which haplotypes were the first to originate and which are the most recently derived haplotypes (Freeland *et al.* 2011). Divergence times were calculated with the *p* statistic (Morral *et al.* 1994) and its standard deviation (Saillard *et al.* 2000) since this statistic can be transformed into years. This statistic is unbiased and highly independent of past demographic events. This approach is called a "borrowed molecular clock" and directly uses the nucleotide substitution rates estimated in other taxa (Pennington and Dick 2010). For the set of three mt genes, we used an evolutionary rate of 1.75 % per million years, representing one mutation every 22,742 years. For all mitogenomic data, the evolutionary rate used was 2.34 % per million years, equivalent to one mutation every 2,638 years. These evolutionary rates were reported for the family Canidae (Wayne *et al.* 1997). In the present work, this methodology was used to estimate divergence times as previous studies (Ruiz-García *et al.* 2020a, 2021a, b) have used Bayesian inference methods to investigate the divergence between the species of *Nasua*, *Nasuella*, and *Bassaricyon*. However, the use of the MJN is preferable because the present study preferably analyzed the divergence times within *N. narica*, and there is a scarce fossil record for coatis. In fact, there are no fossil remains attributable to either *N. narica* or *Nasuella,* and those attributable to *N. nasua* do not exceed 0.125 MYA (Woodburne 2010), which significantly underestimates all studies of divergence times within procionids (Koepfli *et al.* 2007; Nigenda-Morales *et al.* 2019; Ruiz-García *et al.* 2019b, 2020a, 2021a, b).

Genetic heterogeneity and diversity. The statistics H_{ST}, K_{ST}, K_{ST}*, γ_{ST}, N_{ST}, and F_{ST} (Hudson *et al.* 1992) were calculated to determine the global genetic heterogeneity among the six genetic groups of *N. narica* detected with the phylogenetic methods used for both the set of three mt loci and the mitogenomic set. Indirect estimates of the genetic flow between the six genetic groups were obtained assuming an infinite island model (Wright 1965). Statistical significance was estimated using a permutational test with 10,000 replicates. Additionally, genetic heterogeneity and genetic flow statistics were estimated in pairs for the six groups detected. To this end, the F_{ST} statistic was used with Markov chains with 10,000 dememorization parameters, 20 batches, and 5,000 iterations per batch. All analyses were carried out using the DNAsp 5.1 (Librado and Rozas 2009) and Arlequin 3.5.1.2 (Excoffier and Lischer 2010) programs.

We estimated the number of haplotypes (NH), haplotypic diversity (*H*d), nucleotide diversity (π), and the statistic Ø per sequence in the DNAsp 5.1 program (Librado and Rozas 2009) for the total sample and for each of the six genetic groups detected by the phylogenetic analyses.

Spatial autocorrelation analysis. A total of four spatial analyses were applied to the set of three mt loci and three to the set of mitogenomes. The first analysis was a Spatial Analysis of Molecular Variance (SAMOVA) with the SAMOVA 1.0 program (Dupanloup *et al.* 2002) to assess the spatial structure in a geographic context. This program seeks to define geographically homogeneous groups of populations and maximize differentiation with other geographic groups. This would potentially facilitate the identification of genetic barriers between population groups. The method is based on a simulated annealing procedure that helps maximize the proportion of total genetic variance due to differences between population groups. We analyzed the number of different populations (*k*; from two to six), and the statistical significance was estimated with 1,000 permutations.

The second analysis was isolation by distance with the Mantel test (Mantel 1967) performed in the Alleles In Space 1.0 (AIS) program (Miller 2005). The matrix of genetic distances of the Kimura two-parameter model (Kimura 1980) between the different individuals of *N. narica* sequenced was compared with the matrix of Euclidean geographic distances between them. Statistical significance was estimated with 10,000 permutations.

The third procedure was a spatial autocorrelation analysis using the *Ay* statistic with AIS 1.0 (Miller 2005). This can be interpreted as the average genetic distance between pairs of individuals falling within a particular distance class (DC). *Ay* takes a value of 0 when all individuals within a DC are genetically identical and a value of 1 when all individuals within a DC are completely different. The probability for each DC was obtained using 10,000 permutations. To carry out this analysis, we defined 10 DCs constructed using DCs of identical size (in km) with unequal sample size per DC for the set of three mt loci (DC 1: 0–183 km; DC 2: 183–366 km; DC 3: 366–549 km; DC 4: 549–732 km; DC 5: 732–915 km; DC 6: 915–1,098 km; DC 7: 1,098–1,281 km; DC 8: 1,281–1,464 km; DC 9: 1,464–1,647 km; DC 10: 1,647-1,831 km), and 10 DCs constructed with unequal CDs but with approximately the same sample sizes per DC for mitogenomic data (DC 1: 0–26 km; DC 2: 26–83 km; DC 3: 83–183 km; DC 4: 183–270 km; DC 5: 270–337 km; DC 6: 337–381 km; DC 7: 381–547 km; DC 8: 547–730 km; DC 9: 730–1,089 km; DC 10: 1,089–2,298 km). The specimens were connected to the Gabriel and Sokal network (Gabriel and Sokal 1969) and other types of networks (Ruiz-García 1993, 1994, 1997, 1999; Ruiz-García and Álvarez 2000).

The fourth analysis was the Monmonier algorithm (Monmonier 1973; MMDA) with the AIS 1.0 program (Miller 2005). This geographic regionalization method was used to detect putative geographic barriers to gene flow by iterative identification of contiguous sets of high genetic distances across connectivity networks (Doupanloup *et al.* 2002; Manel et al. 2003; Manni *et al.* 2004). The Delaunay triangulation was used (Watson 1992; Brouns *et al.* 2003) to generate the connectivity network between sampling points. A graphic representation of the putative geographic barriers inferred by the algorithm was overlaid on the connectivity network to facilitate the detection of likely geographic obstacles reflected in the sequence data. In this case, the procedure was used to identify the five most important possible putative geographic barriers for the set of three mt loci.

Results

Phylogenetic analysis for three mitochondrial loci and for complete mitogenomes. The optimal nucleotide substitution models for the set of three mt loci were TN93 + G for CIA (-Ln = 11,861.36) and GTR + G + I for CIB (-Ln = 17,332.27); for the mitogenomic set, the optimal nucleotide substitution model was GTR + G + I for CIA (-Ln = 55,535.88) and TN93 + G for CIB (-Ln = 63,912.52). For the phylogenetic analyses, we used the GTR + G + I model since it was one of the two optimal models in all cases and is a model implemented in the programs used.

In the ML tree (Figure 2) with three mt loci, the *N. nasua* clade had good nodal support and was the sister group of the other clades (Bootstrap Support, BS = 100). An interesting finding is the inclusion in this clade of three specimens that *a priori* would correspond to *N. narica* based on their phenotype and geographic origin. The first is a specimen from Robinson Crusoe Island (Chile). The other two specimens were collected in northern Colombia. In both cases, the analysis with three mt genes showed that they were highly related (BS = 95). The remaining clades found in *N. nasua* were already analyzed in detail by Ruiz-García *et al.* (2021a).

The clade of *N. olivacea* also had high nodal support (BS = 95) and was the sister group of *N. narica*; this may be considered evidence that the genus *Nasuella* could be included in the genus *Nasua* (Ruiz-García *et al.* 2021b). On the other hand, a group of five specimens of *N. narica* distributed in southern Costa Rica, Panama, and northern Colombia (Antioquia and Choco) — the typical distribution of *N. narica* — with an undoubted morphotype of this species, nested within the *N. olivacea* clade. This group (BS = 72), which we named G6, has a mitochondrial DNA clearly introgressed by *N. olivacea*.

The *N. narica* group was monophyletic (BS = 74) and was composed of five distinct genetic groups. The first (G1; BS = 79) comprised two specimens from the trans-Andean (Pacific) part of Ecuador (Guayas province). The second group (G2; BS = 97) is composed of two specimens sampled in Yucatán (México). The third genetic group (G3; BS = 81) is formed by specimens sampled in northern Costa Rica, Nicaragua, El Salvador, Honduras, and southern Guatemala. It should be noted that an Ecuadorian Amazonian specimen with the phenotype of *N. narica* (Macas, province of Morona-Santiago) was included in this clade. The fourth group (G4; BS = 91) consisted of specimens distributed in the northwestern part of Guatemala and Belize; however, two specimens from the Pacific coast of Ecuador (Guayas province) were also included in this group. Finally, the fifth genetic group (G5; BS = 90) comprised specimens from northwestern Guatemala and southern México, with specimens from Quintana Roo (including Cozumel Island), Campeche, Chiapas, Tabasco, and Yucatán.

The ML tree (Figure 3) with mitogenomic data was similar to the previous one, with minor differences. *Nasua nasua* was the sister clade of all others (BS = 87). The specimen from Robinson Crusoe Island (Chile) was included in this taxon. Contrary to the ML tree calculated with three mt loci, one specimen of *N. narica* from central-northern

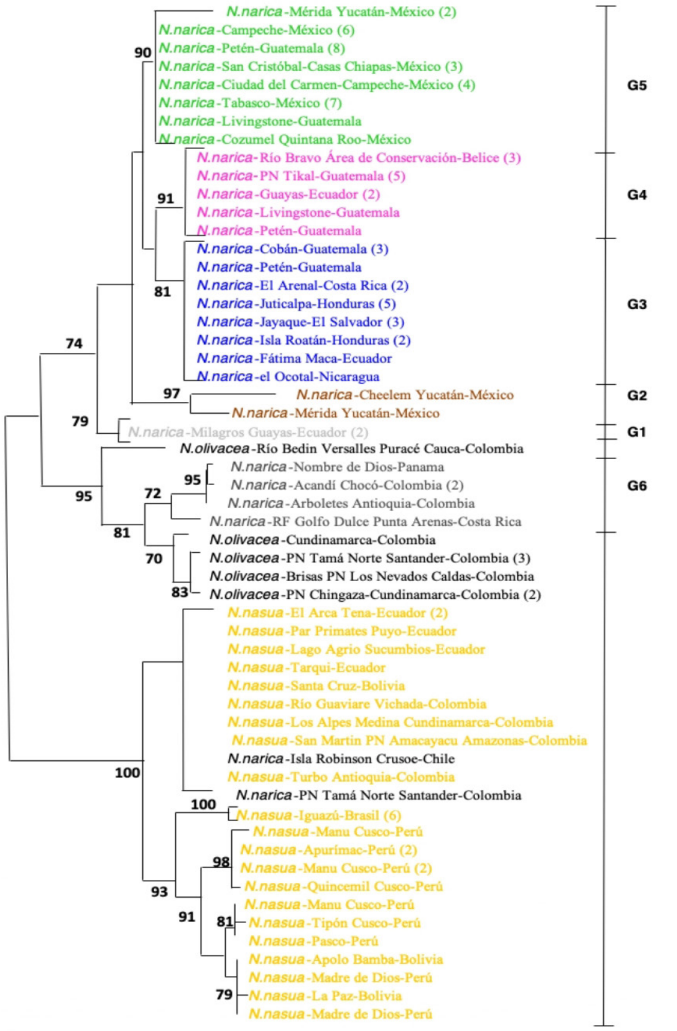

Figure 2. Maximum Likelihood Tree showing the phylogenetic relationships of 74 specimens of white-nosed coati (*Nasua narica*) for three mitochondrial genes (*ND5, Cyt-b*, and *D-loop*). The mountain or Andean coati, *Nasuella olivacea*, and the South American coati, *Nasua nasua,* were used as external groups. Numbers on nodes are bootstrap percentages greater than 70 %. The number of specimens sampled in a given locality is shown in parenthesis.

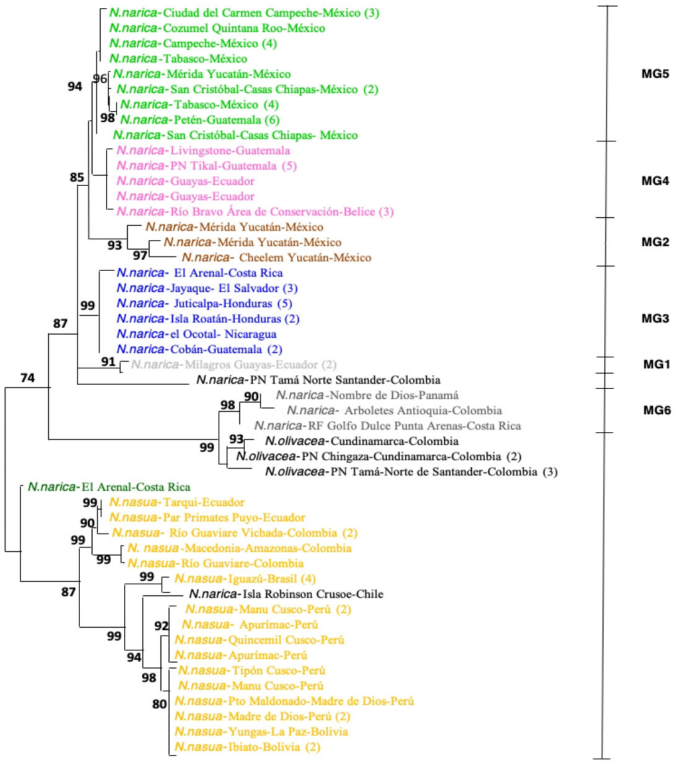

Figure 3. Maximum Likelihood Tree constructed with the complete mitogenomes of 59 specimens of white-nosed coati (*Nasua narica*). The mountain or Andean coati (*Nasuella olivacea*) and the South American coati (*Nasua nasua)* were used as external groups. Numbers on nodes are bootstrap percentages greater than 70 %. The number of specimens sampled in a given locality is shown in parenthesis.

Costa Rica was shown to be the most divergent within the *N. nasua* clade. The *N. olivacea* clade (BS = 99) was the sister group of *N. narica* (BS = 87); it included the genetic group (MG6) of *N. narica* (BS = 98), with which the complete mitogenomes confirmed the genetic introgression of one group of *N. olivacea* in the distribution range of *N. narica* in southern Central America and northern Colombia. In the present tree, the specimen from PN Tamá (North of Santander, Colombia) forms a polytomy with the genetic groups MG1 (BS = 91) and MG3 (BS = 99). This was followed by the subsequent divergence of groups MG2 (BS = 93; in this case, a third specimen from the Yucatán Peninsula was added, which had been included in G5 in the previous tree), MG4 (BS = 85), and MG5 (BS = 94).

The haplotype network (Figure 4) for the set of three mt loci showed that the earliest ancestral *N. narica* haplotypes would have derived from *N. nasua* haplotypes; these specimens already displayed the distinctive phenotype of *N. narica* and with haplotypes very close to one of the external groups. These were found in the trans-Andean and Pacific zones of Ecuador (H2 and H4), along with the haplotype of the specimen from the Ecuadorian cis-Andean (Amazon) zone (H3) that had been included in G3 in the phylogenetic trees for the three mt loci. In other words, the first *N. narica* (with explicit phenotypes of this species) with haplotypes already differentiated from those of *N. nasua* and closer to the Central American *N. narica* are found in Ecuador, in the

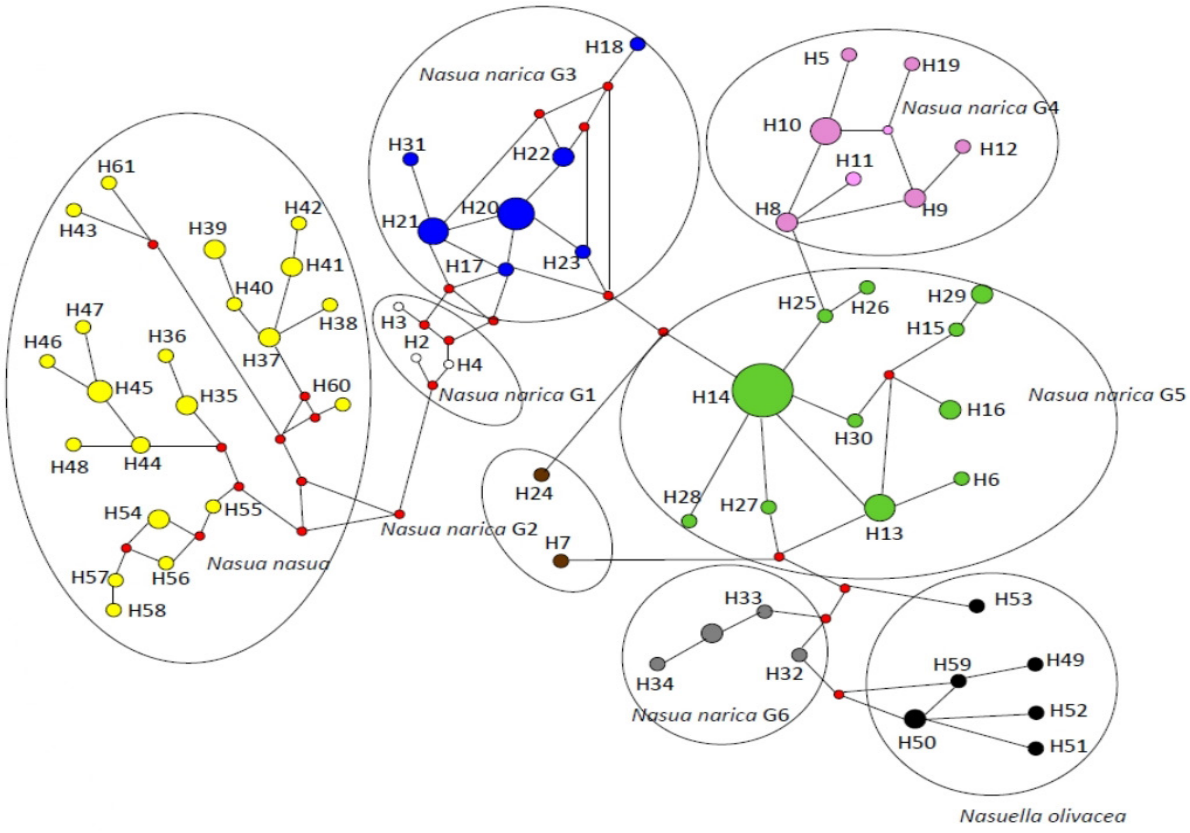

Figure 4. Median Joining Network procedure applied to the haplotypes found in 74 specimens of white-nosed coati (*Nasua narica*) for three mitochondrial genes (*ND5*, *Cyt-b*, and *D-loop*). The haplotypes of eight mountain or Andean coatis (*Nasuella olivacea*) and 29 South American coatis (*Nasua nasua*), were used as external groups. White = haplotypes of G1 specimens; brown = haplotypes of G2 specimens; blue = haplotypes of G3 specimens; pink = haplotypes of G4 specimens; light green = haplotypes of G5 specimens; gray = haplotypes of G6 specimens; black = haplotypes of *N. olivacea* specimens; yellow = haplotypes of *N. nasua* specimens; small red circles indicate intermediate haplotypes that were not found.

trans-Andean and cis-Andean areas (G1). From this group (haplotypes that were gradually differentiated from the external group), G3 would have emerged, distributed in the south-central zone of Central America, with H20 occupying the central position in the analysis (El Salvador, Honduras, and southern Guatemala). G5 would have later derived from G3, with H14 at the central position in the analysis (northern Guatemala and México, including Chiapas, Tabasco, Campeche, and part of Yucatán). G4 derived from G5 (northwestern Guatemala and Belize, although these groups also included haplotypes from the trans-Andean zone of Ecuador). Finally, G6 clearly showed that it was introgressed by *N. olivacea*, as reflected by phylogenetic trees. In this network of haplotypes, G2, clearly visible in the trees mentioned above, does not form a well-consolidated group. One haplotype (H24) appears as derived from a non-sampled haplotype between G3 and G5, and another haplotype (H7) appears as derived from G5.

Divergence times within and between N. narica *groups.* For the matrix of three mt loci, using the MJN, the time elapsed for the G1 haplotype to give rise to all the Central American haplotypes derived from it was 4.06 ± 0.93 million years ago (Mya). On the other hand, for the mitogenomic data set, the divergence between the intermediate haplotype of the *N. narica* specimen from central-northern Costa Rica and all other Central American haplotypes detected occurred 3.16 ± 0.34 Mya. The time elapsed since G1 gave rise to the first G3 haplotype was estimated at 2.20 ± 0.27 Ma for the set of three mt loci and 1.21 ± 0.02 Mya between the intermediate Costa Rican haplotype and the first MG3 haplotype, respectively. The time of divergence since the G3 generated all the other northernmost haplogroups in Central America was 1.93 ± 0.54 Mya and the time between the G3 haplotype and the emergence of G5 from it was 1.07 ± 0.30 Mya. The same divergence times with mitogenomic data were 0.82 ± 0.15 Mya and 0.36 ± 0.01 Mya, respectively. The time elapsed since G5 gave rise to the first G4 haplotype was estimated at 0.12 ± 0.27 Mya for the set of three mt loci and 0.09 ± 0.02 Mya for the mitogenomic set, respectively. Additionally, the time of divergence between the nearest *N. narica* haplotypes and the *N. narica* haplotypes introgressed by *N. olivacea* was 4.4 ± 0.15 Mya for the set of three mt loci and 2.34 ± 0.08 Mya for the mitogenomic set, respectively. Finally, the temporal separation between the present *N. olivacea* haplotypes and those of G6 (MG6) (*N. narica* introgressed by the latter species) was 2.32 ± 0.34 Mya for the set of three mt loci and 0.73 ± 0.08 Mya for the mitogenomic data. In general, for most estimates, the divergence times estimated with mitogenomic data are shorter than those estimated with the set of three mt loci. Additional divergence times are shown in Table 1.

Genetic heterogeneity and diversity within and among Nasua narica *groups.* The analysis of genetic heterogeneity for the six genetic groups of *N. narica* detected from phylogenetic analyses for the matrix of three mt loci showed a significant global genetic differentiation (γ_{ST} = 0.734, p < 0.0001; F_{ST} = 0.658, p < 0.0001; Table 2). The global genetic flow estimates showed low values among these groups, taken globally ($Nm_{\gamma ST}$ = 0.18; Nm_{FST} = 0.26). The same analysis including only the four Central American groups (excluding G1 and G6) also showed high and significant values (γ_{ST} = 0.599, p < 0.0001; F_{ST} = 0.496, p < 0.0001; Table 2), and genetic flow estimates were also low ($Nm_{\gamma ST}$ = 0.33; Nm_{FST} = 0.51). These results are consistent with the mitogenomic data (γ_{ST} = 0.755, p < 0.00001; F_{ST} = 0.775, p < 0.00001; Table 2), with low genetic flow values ($Nm_{\gamma ST}$ = 0.16; Nm_{FST} = 0.14).

The analysis of paired genetic heterogeneity of genetic groups with data from three mt loci showed that all comparison pairs were significant (Table 3), except for the pair G1 vs. G2 (p = 0.331). The highest genetic flow was estimated between G1and G2 (Nm = 0.504) and the lowest between G3 and G6 (Nm = 0.038; Table 4). The mitogenomic data showed similar results. The only pair of groups with a nonsignificant difference was between MG1 and MG2 (p = 0.103; Table 3). The highest estimate of genetic flow was between the pair of groups MG1 and MG2 (Nm = 0.578) and the lowest between G5 and G6 (Nm = 0.021; Table 4). Therefore, there is very high genetic heterogeneity among the six groups detected with phylogenetic methods.

The levels of global genetic diversity for both three-loci-based data and mitogenomic data (Supplementary Table 2) are high. By group, G1 (MG1), G2 (MG2), and G6 (MG6) showed the highest levels of genetic diversity for both the three-loci mt matrix and the mitogenomic matrix. The groups that showed the lowest levels of genetic diversity were G3 and G5 for both the data with three mt loci and mitogenomic data.

Spatial structure in N. narica. With the three mt loci, the maximum differentiation was observed between four groups (F_{CT} = 0.702, p < 0.0001), *i. e.*, G6, G1, G2, and the set of G3, G4, and G5. With mitogenomes, the maximum differentiation occurred between two groups (F_{CT} = 0.817, p < 0.0001), namely, between MG6 and all the other groups of *N. narica*, regardless of their geographic location (Supplementary Table 3).

Table 1. Divergence times within the different groups of white-nosed coati (*Nasua narica*) detected through its geographic distribution range in Central America and northern South America. A) Based on three mitochondrial genes (*ND5, Cyt-b*, and *D-loop*); B) based on complete mitogenomes. SD = Standard Deviation. Time in millions of years.

Groups of *Nasua narica*	Divergence Times ± SD
A	
Within G1	2.99 ± 0.69
Within G3	0.25 ± 0.11
Within G4	0.49 ± 0.18
Within G5	0.60 ± 0.13
Within G6	2.47 ± 0.77
B	
Within MG1	1.34 ± 0.16
Within MG3	0.15 ± 0.04
Within MG4	0.41 ± 0.09
Within MG5	0.12 ± 0.03
Within MG6	0.37 ± 0.09

Table 2. Statistics of genetic heterogeneity and gene flow comparing simultaneously the different groups of white-nosed coati (*Nasua narica*) detected in Central America and northern South America. A) Based on three mitochondrial genes (*ND5, Cyt-b*, and *D-loop*) for six different groups (four in Central America and two in northern South America); B) based on three mitochondrial genes (*ND5, Cyt-b*, and *D-loop*) for four groups in Central America; C) based on mitogenomes for all groups detected. ** $p < 0.01$, *df* = degrees of freedom. *Nm* = Gene Flow statistic. Nm^1 = Gene flow obtained with the γ_{ST} statistic; Nm^2 = gene flow obtained with the N_{ST} statistic; Nm^3 = gene flow obtained with the F_{ST} statistic.

Genetic Heterogeneity and gene flow statistics	Values	Probabilities
A		
X^2	360.000 *df* = 165	0.00001**
H_{ST}	0.1732	0.00001**
K_{ST}	0.6718	0.00001**
K_{ST}*	0.5162	0.00001**
Z_S	492.11	0.00001**
Z_S*	5.8609	0.00001**
S_{nn}	0.9563	0.00001**
γ_{ST}	0.7344	0.00001**
N_{ST}	0.6689	0.00001**
F_{ST}	0.6578	0.00001**
Nm^1	0.18	
Nm^2	0.25	
Nm^3	0.26	
B		
X^2	195.000 *df* = 81	0.00001**
H_{ST}	0.1651	0.00001**
K_{ST}	0.5269	0.00001**
K_{ST}*	0.4456	0.00001**
Z_S	465.6	0.00001**
Z_S*	5.8262	0.00001**
S_{nn}	0.967	0.00001**
γ_{ST}	0.5995	0.00001**
N_{ST}	0.4963	0.00001**
F_{ST}	0.4956	0.00001**
Nm^1	0.33	
Nm^2	0.51	
Nm^3	0.51	
C		
X^2	996.000 *df* = 240	0.00001**
H_{ST}	0.0112	0.00069**
K_{ST}	0.7068	0.00001**
K_{ST}*	0.3718	0.00001**
Z_S	2262.6	0.00001**
Z_S*	5.211	0.00001**
S_{nn}	0.9464	0.00001**
γ_{ST}	0.755	0.00001**
N_{ST}	0.7862	0.00001**
F_{ST}	0.7755	0.00001**
Nm^1	0.16	
Nm^2	0.14	
Nm^3	0.14	

The results of the Mantel test were significant for the matrices of three mt loci and mitogenomes. In the first case, geographic distance significantly explained 30.59 % of the genetic distances between the specimens analyzed (r = 0.553, p = 0.00009); in the second, geographic distance significantly explained 23.81 % of genetic distances (r = 0.488, p = 0.0014). In general, evidence of isolation by distance was detected in the geographic distribution of *N. narica*.

The spatial autocorrelation analysis showed evidence of spatial structure. For the matrix with three mt loci, the global correlogram was statistically significant (V = 0.0361, $p < 0.000001$). The first two distant classes (DCs) showed a significant positive spatial autocorrelation (DC 1: p = 0.000001; DC 2: p = 0.000001). This indicates that in areas around 360 km in in diameter there are specimens more genetically similar to each other than expected at random. From DC 6, all spatial autocorrelation values were significantly negative (DC 6: p = 0.0021; DC 7: p = 0.0026; DC 8: p = 0.0001; DC 9: p = 0.0003; DC 10: p = 0.0002). That is, from 1,098 km to 1,831 km, genetic differentiation progressively increased. Similar results were obtained with mitogenomic data. The overall correlogram was statistically significant (V = 0.0146, $p < 0.0008$), with the first six DCs showing a significant positive spatial autocorrelation (DC 1: p = 0.00001; DC 2: p = 0.026; DC 3: p = 0.0175; DC 4: p = 0.0338; DC 5: p = 0.000001; DC 6: p = 0.0365). This indicated a strong genetic similarity between specimens geographically separated by a distance of about 380 km between them. This value is very similar to the one reported above for the first spatial autocorrelation analysis. DCs 9 and 10 yielded a significant negative spatial autocorrelation (DC 9: p = 0.0071; DC 10: p = 0.0023). That is, genetic differentiation increased from 729 km to 2,297 km. Therefore, both analyses show a clear monotonic cline in northern South America and Central America.

The analysis with the Monmonier algorithm (Figure 5) was performed for only three mt loci. The first barrier detected differentiated the geographic area corresponding to G6 specimens introgressed by *N. olivacea*. The second barrier demarcated a geographic area correlated with the area where part of the G4 specimens are interspersed (Belize) with part of the G5 specimens (Cozumel Island and part of Yucatán). The third barrier bordered the geographic area corresponding to G2 specimens (Yucatán). The fourth barrier delimited the geographic area that included G1 specimens (Ecuadorian Pacific). The fifth barrier marked the geographic area that was aligned with the trans- and cis-Andean zones of Ecuador but with specimens more genetically related to the Central American group G3. The geographic structure of *N. narica* in Central America and northern South America is very pronounced.

Discussion

Systematics of N. narica. This article reports the population phylogeographic and genetic analysis encompassing the broadest geographic extension of the distribution range of *N. narica* to date and uses complete mitogenomes for this species for the first time. From a strictly systematic standpoint, this analysis provides new evidence for the re-interpretation of the systematics of this species.

The genetic distances between the different *N. narica* groups found are smaller than those observed in *N. nasua* (Ruiz-García *et al.* 2020a, 2021a). The values ranged from 1.6 % to 4.5 %, typical of well-differentiated populations or subspecies (Kartavtsev 2011). This is consistent with the fact that the ancestor of the present *N. narica* is considerably more recent than the ancestor of the present *N. nasua*, which, in turn, shows that the mitochondrial evolution of coatis occurred in South America in the first place and then in Central America. This conclusion contrasts with the traditional paleontological view that the current coatis migrated from North to South America in the early Pleistocene. The arrival of the first procionids in South America produced endemic forms (Argentina) such as *Cyonasua* and *Chapalmalania* (Soibelzon and Prevosti 2013) around 7.3 Mya. However, paleontologists consider that these procionids became extinct and did not give rise to the present *Nasua*. They are considered to have arrived in South America in a second migratory wave of procionids during GABI 4 (Woodburne 2010), which occurred during the Lujanense (126,000–8,500 before present, BP) and Platense (8,500–1,500 BP) ages. However, *N. nasua* haplotypes started to differentiate *in situ* in northwestern South America some 13–10 Mya (Ruiz-García *et al.* 2020a, 2021a, b), preceding the diversification of *N. narica* haplotypes (also in northwest South America) 4.1–3.2 Mya. These findings indicate a south-to-north migration of the current coatis, opposite to the direction suggested by paleontologists.

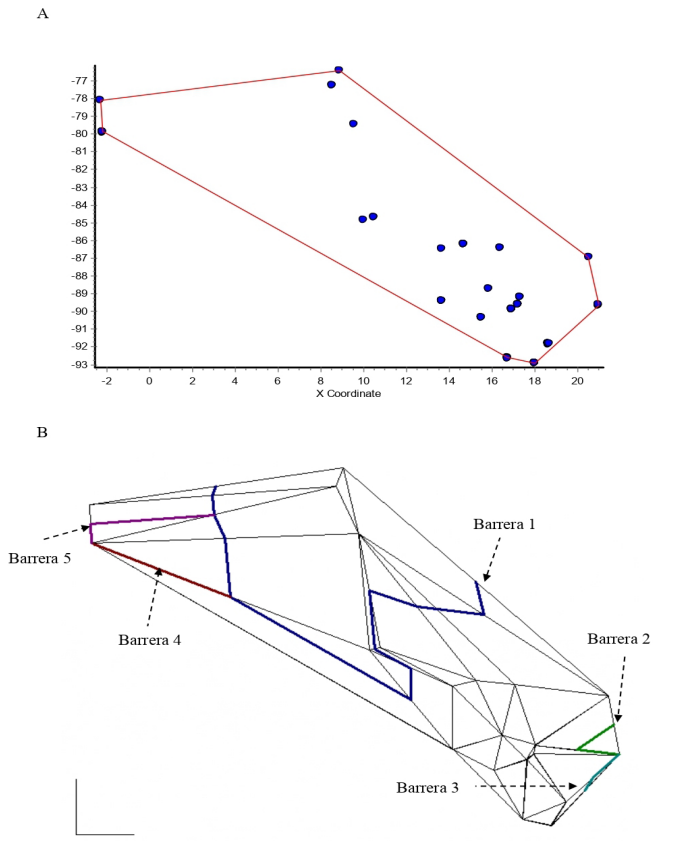

Figure 5. Analysis of the Monmonier algorithm to detect the five most important geographic barriers in the geographic distribution range of the samples of white-nosed coati (*Nasua narica*) analyzed from Central America and northern South America. A) Geographic area analyzed; B) Geographic barriers for 74 specimens of *N. narica* sequenced for three mitochondrial genes (*ND5, Cyt-b*, and *D-loop*).

Four morphological subspecies of *N. narica* have been considered in recent decades (Gompper 1995): *N. n. molaris*, *N. n. nasua*, *N. n. nelsoni*, and *N. n. yucatanica*. In particular, *N. n. nelsoni* has been considered a full species (*N. nelsoni*). However, the present study showed at least six genetically distinct groups.

The first group (G1, MG1) is distributed in northwestern South America. We have detected haplotypes of this group in the Ecuadorian Pacific and, in the mitogenomic study, also in one specimen from northern Colombia (PN Tamá, North of Santander). Traditionally, the coatis of the trans-Andean and Pacific Colombian and Ecuadorian areas have been classified as *N. narica* (Emmons 1990; Emmons and Feer 1997; Tirira 2007, 2011); however, some authors (Gompper 1995; Nowak 1999) suggest that the coati living in the Pacific area of Colombia and Ecuador is *N. nasua* based on its morphological traits.

Our research showed that some of those specimens might be intermediate forms between *N. nasua* and *N. narica*. The specimens in this group from the Ecuadorian Pacific had external phenotypes (coloration and fur pattern) typical of *N. narica*. However, Ruiz-García *et al.* (2021a) observed that most specimens with the *N. narica* phenotype in the trans-Andean and Pacific areas of Ecuador had the mitochondrial haplotypes typical of *N. nasua*. The study also detected specimens in the Ecuadorian Pacific with intermediate morphotypes between *N. nasua* and *N. narica*. That study also showed that the *N. narica* haplotypes of the Ecuadorian Pacific and North Santander (Colombia) had originated from an *N. nasua* haplotype distributed in the Colombian and Ecuadorian Amazon. One specimen from the Colombian Pacific (not included in this study; Buenaventura, Valle del Cauca) with an intermediate phenotype between *N. narica* and *N. nasua* showed inconclusive results according to different molecular analyses performed (Ruiz-García *et al.* 2021a). In fact, in the present study, we detected one specimen of PN Tamá (located in an area where *N. nasua* and *N. narica* allegedly converge), which, despite having the distinct *N. narica* morphotype, resembled *N. nasua* in the analysis with three mt genes (not so in the mitogenomic analysis). The analysis with three mt genes also included one specimen (Turbo, Antioquía, Colombia; border area between Colombia and Panama) with a morphotype closer to *N. nasua* but within a distribution area typical of *N. narica*. The analysis based on three mt loci associated this specimen with the previous specimen within the *N. nasua* clade. Unfortunately, that specimen could not be sequenced for its complete mitogenome because of the poor quality of its DNA. However, there is evidence on the Pacific coast of Ecuador and Colombia, and in northern Colombia, of specimens with a full *N. narica* morphotype and with mitochondrial haplotypes intermediate between *N. nasua* and Central American *N. narica*, albeit closer to the latter. Ruiz-García *et al.* (2020a, 2021ab) showed that the haplotypes of *N. nasua* and *N. olivacea* diverged in South America before those of *N. narica*. The

Table 3. F_{ST} statistic for paired groups of white-nosed coati (*Nasua narica*) analyzed in Central America and northern South America. Below the diagonal, based on three mitochondrial genes (*ND5, Cyt-b*, and *D-loop*) (G); above the diagonal, based on mitogenomes for all groups detected (MG). * $p < 0.05$; ** $p < 0.01$.

Groups of *Nasua narica*	G1 (MG1)	G2 (MG2)	G3 (MG3)	G4 (MG4)	G5 (MG5)	G6 (MG6)
G1 (MG1)		0.463	0.786**	0.564*	0.803**	0.910
G2 (MG2)	0.498		0.734**	0.629**	0.723**	0.823
G3 (MG3)	0.822**	0.833**		0.697**	0.723**	0.952**
G4 (MG4)	0.771**	0.788*	0.764**		0.578**	0.928**
G5 (MG5)	0.817**	0.834**	0.652**	0.615**		0.960**
G6 (MG6)	0.849*	0.810*	0.928**	0.912*	0.735*	

existence of intermediate haplotypes between *N. nasua* and *N. narica* are particularly well-detected in the haplotype networks of the Ecuadorian Pacific and northern Colombia.

The case of the assumed *N. narica* from Robinson Crusoe Island in the Chilean Pacific might represent a hybridization event. In the 1950s, a couple of Germans introduced coatis to fight rodent pests on the island. The morphotype of these island animals matches *N. narica*. However, this study, together with that of Ruiz-García *et al.* (2021a), showed that the mtDNA of that specimen behaved like *N. nasua*. The coatis introduced to those islands likely came from the Ecuadorian Pacific with the typical phenotype of *N. narica* but with the mtDNA of *N. nasua* that characterizes part of the coatis inhabiting the Pacific slope of Ecuador.

The problem with *N. narica* from Ecuador and Colombia is that they have not been assigned a sub-specific denomination because it has recently been considered that this species is not present in the Pacific zone of these two countries. It would be very important to perform morphological and molecular analyses of the *N. nasua* holotypes or paratypes described for the trans-Andean and Pacific areas of Ecuador. The holotype described for this Ecuadorian area was first named *N. nasua manium* (Thomas 1912), but a more recent paratype was also described for the same area, *N. nasua gualeae* (Lönnberg 1921; Type locality: Gualea, province of Pichincha, Ecuador). If either of these two taxa could be analyzed at molecular level and had *N. narica* mtDNA, then the G1 (MG1) specimens could be assigned to *N. narica manium* or *N. narica gualeae*, with preference for the first name.

Therefore, our results drastically change the traditional view of the existence of only *N. narica* on the Colombian and Ecuadorian Pacific coast and challenge the idea of the absence of this species in that geographic area, as claimed by other authors (Gompper 1995; Nowak 1999). Indeed, most coatis living in the Pacific trans-Andean zone of Colombia and Ecuador belong to *N. nasua*. However, a small proportion of individuals in this geographic area show the oldest *N. narica* haplotypes found to date with a morphotype very similar to the Central American populations (present study and Ruiz-García *et al.* 2021a). Additionally, in the Ecuadorian Pacific, we detected two specimens (for the set of three mt loci, only one for mitogenomes) with the *N. narica* phenotype and the typical Central American G4 (MG4) haplotypes. Furthermore, an Ecuadorian cis-Andean animal (Macas, Morona-Santiago province, Ecuadorian Amazon) showed the typical Central American G3 haplotype. This would indicate that an *N. narica* haplotype would have crossed the Andes mountain range; however, we currently ignore whether this crossing was natural or resulted from humans transporting animals through the Ecuadorian Andean Cordillera. The fact that the Macas specimen showed a haplotype with some nucleotide differentiation relative to the G1 haplotypes leads us to think that the crossing of the Cordillera was not recent, likely a natural process.

Therefore, nuclear genes should be analyzed to determine the degree of hybridization or introgression (if any) between the small proportion of coatis with *N.* aff. *narica* phenotype and mtDNA (defined in this study as *N. narica*) and the largest proportion of specimens, many of them also with phenotypes with *N. narica* traces but with mtDNA belonging to different *N.* aff. *nasua* haplogroups (defined herein as *N. nasua*), especially in the Ecuadorian area considered. Nuclear DNA sequencing could contribute to defining the coati systematics. Additionally, our results indicate that in the Pacific area and northern Colombia there is another group of *N. narica* (G6, MG6) introgressed with mtDNA of *N olivacea*. These new findings are relevant to the conservation policies of coatis in Colombia and Ecuador.

In Central America, the situation would be as follows: 1) *N. n. molaris*, from the north-central and Pacific areas of México to southern USA, was not represented in our samples. However, Silva-Caballero *et al.* (2017) showed with the mt *Cyt-b* gene, on the one hand, a clade including the haplotypes of the Mexican Pacific coast (Punta Raza and Chamela-Cuixmala, Nayarit and Jalisco, respectively) and, on the other hand, a clade comprising the haplotypes of central México (El Tepozteco; Morelos) and southeast México (La Venta and Puerto Morelos, Tabasco and Quintana-Roo, respectively). In fact, the highest F_{ST} statistic was between one of the Pacific populations (Chamela-Cuixmala) and the central population (El Tepozteco; $F_{ST} = 0.125$, $p < 0.05$). The same trend was observed with nuclear microsatellites. With the R_{ST} statistic (0.995; $p < 0.05$), the most differentiated populations were those of Chamela-Cuixmala (Mexican Pacific) and Puerto Morelos in the Yucatán Peninsula; with the F_{ST} statistic 0.258; $p < 0.05$), the most differentiated populations were Punta Raza (Mexican Pacific) and El Tepozteco (Central México). Likewise, Nigenda-Morales *et al.* (2019) detected five distinct groups in the sample of *N. narica* studied with both mitochondrial sequences

and nuclear microsatellites. Three of these groups were detected in the geographic area attributed *a priori* to *N. n. molaris*. These three groups were distributed in the Mexican Pacific, Central México, and southwestern United States. The *N. n. molaris* holotype comes from Colima in the Mexican Pacific. Therefore, the Mexican Pacific group can be related to *N. n. molaris*. In contrast, the other two groups found by Nigenda-Morales *et al.* (2019) in central-northern México and southwestern USA may correspond to *pallida* (Allen 1904), *tamaulipensis* (Goldman 1942), *vulpecula* (Erxleben 1777), or *solitaria* var. *mexicana* (Weinland 1860); the respective holotypes should be analyzed to confirm those denominations. 2) *N. n. narica*, whose holotype comes from the State of Veracruz corresponds well with our fifth genetic group (G5, MG5). It also corresponds to one of the groups detected by Nigenda-Morales *et al.* (2019) in the Yucatán Peninsula and Guatemala. 3) *N. n. yucatanica*, whose holotype comes from "Merida in the Yucatán Peninsula", may be represented by our second genetic group (G2, MG2). However, this group, which comprises a few specimens, shows a high internal genetic heterogeneity and a variable relationship with other groups according to the analyses used. An extensive molecular study is needed in the Yucatán and north Quintana Roo since this area appears to have a highly marked genetic structure at the micro-geographic level. We have detected specimens in the area of Mérida separated by a few kilometers, belonging to groups G2 and G5, suggesting the possibility of areas with hybrid specimens of these two groups in that Mexican state. 4) *N. n. nelsoni* or *N. nelsoni* is typical of Cozumel Island. We only studied one specimen from this area, which was included in G5. Likewise, Nigenda-Morales *et al.* (2019) analyzed nine specimens from this island and found no obvious differentiation between these specimens and those from the Yucatán and north Guatemala discussed above. Therefore, molecular evidence seems to reject the validity of *N. n. nelsoni* (*N. nelsoni*). The only possibility for this taxon to be valid is that the specimen studied by us, and the nine specimens analyzed by Nigenda-Morales *et al.* (2019) had been recently introduced by human activities from southern México to Cozumel, and that an original population persists in the island, which had not been sampled in either of the two works. Otherwise, this taxon would have no systematic validity since it could have been introduced to the island in relatively recent historical times. The smaller body size of the coati of Cozumel Island may have been generated over a few generations through natural selection as an adaptation to a small island with few food resources. We agree with Glatston (1994) that this coati was introduced to Cozumel by the Mayans, although we do not agree that *N. nelsoni* is a full species. Similarly, the coati sampled on Roatán Island (Honduras) had the same haplotype as the others found in G3 (MG3), suggesting that it was recently introduced in that locality by human action.

However, three of the genetic groups detected here (and one of those found by Nigenda-Morales *et al.* 2019, which corresponds to our G6-MG6) do not match any putative morphological subspecies of *N. narica*. Two of these groups, G3 and G4, were not observed by Nigenda-Morales *et al.* (2019) because these authors did not collect samples in Honduras, southern Guatemala, El Salvador, Nicaragua, and Costa Rica (only a single specimen was analyzed). Thus, the subspecific name for these two groups remains to be established. A more complex matter is the likely subspecies designation of G6 (MG6). This group, distributed across southern Costa Rica, Panama, and the border area between northern Colombia and Panama, is introgressed with mt DNA of *N. olivacea*. We propose an ancient introgression with mtDNA from *N. olivacea* to the genetic stock of *N. narica* in the border zone between South America and the south of Central America. In the first place, this hypothesis is supported, by the MJN analysis showing a temporal separation between G6 (MG6) haplotypes and *N. olivacea* haplotypes, both located in the same clade at 2.3 Mya for the set of three mt loci and 0.8 Mya for the mitogenomic set. Secondly, the introgressed specimens lack an intermediate morphotype between *N. narica* and *N. olivacea*, but showed the typical morphotype of *N. narica*. Third, the five specimens studied in southern Costa Rica, Panama, and the area bordering Colombia, and the 13 specimens analyzed by Nigenda-Morales *et al.* (2019), showed *N. olivacea* mtDNA in all cases. If a recent hybridization event had caused this phenomenon, we would expect the *N. olivacea* mtDNA in one specimen, but not in all specimens sampled in that area. A possible subspecific denomination could be *N. narica panamensis* (Allen 1904). However, only molecular analysis of the respective holotype may solve this issue because an alternative possibility is that this subspecific denomination may correspond to G3.

In summary, considering Nigenda-Morales *et al.* (2019) and the present study, at least nine genetically differentiated *N. narica* groups are detectable across its geographic range. Three of the morphological subspecies described

Table 4. Estimated gene flow between six groups of white-nosed coati (*Nasua narica*) analyzed in Central America and northern South America. Below the diagonal, based on three mitochondrial genes (*ND5*, *Cyt-b*, and *D-loop*) (G); above the diagonal, based on mitogenomes for all groups detected (MG).

Groups of *Nasua narica*	G1 (MG1)	G2 (MG2)	G3 (MG3)	G4 (MG4)	G5 (MG5)	G6 (MG6)
G1 (MG1)		0.578	0.136	0.387	0.122	0.049
G2 (MG2)	0.504		0.182	0.295	0.182	0.107
G3 (MG3)	0.108	0.100		0.218	0.191	0.025
G4 (MG4)	0.148	0.134	0.155		0.365	0.039
G5 (MG5)	0.118	0.099	0.267	0.312		0.021
G6 (MG6)	0.088	0.117	0.038	0.048	0.041	

would match three of the genetic groups mentioned, one morphological subspecies described should be invalid, and six new subspecific names should be proposed. The large number of groups found in the present study may respond to different geographic, geological, and ecological causes. In the case of coatis, their behavior is also relevant since they have high levels of phylopatry and a limited dispersal capacity (Frantz *et al.* 2010). They form groups with a small territorial range of 0.5 to 4 km^2 (Valenzuela and Ceballos 2000; Hirsch and Gompper 2017). Being barely dispersed from the birth site, the groups, mainly formed by females, are strongly bonded. Occasionally, males that moved up to 20 km away from their birth sites have been detected (Lanning 1976). However, estimates of gene flow between populations in México (Silva-Caballero *et al.* 2017) or Central and South America (Nigenda-Morales *et al.* 2019 and the present study) show that the coati groups are virtually genetically isolated.

Colonization dynamics and evolutionary times of the different N. narica *groups found.* The results obtained are useful for reconstructing the evolutionary history of *N. narica*; to this end, different hypotheses are proposed regarding the origin of each of the *N. narica* groups detected. The analysis of three mt loci suggests the following colonization schemes: 1) The first group to emerge was the Ecuadorian (G1) (→ = gave rise), which gave rise to two separate colonization events in Central America. The oldest was of G1 → Yucatán Peninsula (G2) and, on the other hand, G1 → south-central Central America (G3) (northern Costa Rica, Nicaragua, El Salvador, Honduras, and part of Guatemala). G3 → G4 (southern Guatemala and Belize) → G5 (northern Guatemala and southern México). In this hypothesis, some differential nuances can be considered to explain the existence of two Ecuadorian trans-Andean specimens in G4 and one Ecuadorian cis-Andean specimen in G3. There are two alternatives. The first is that the oldest haplotypes of G3 and G4 were generated *in situ* in South America, followed by subsequent colonization events to Central America. Some of the original haplotypes that expanded through Central America would still "survive" in the Ecuadorian trans-Andean area. The second is that these haplotypes of G3 and G4 emerged *in situ* in Central America from G1, but there was a subsequent migration of individuals with haplotypes originating in Central America, again, to South America. Besides, in northern South America, an *N. narica* group was introgressed with mt DNA of *N. olivacea* and another colonization event took place from northern South America to southern Central America. This hypothesis is consistent with three mitochondrial colonization events from northern South America to Central America, with the G5 haplotypes (southern México and northern Guatemala) being the most recent ones and the G1 haplotypes (Pacific coast of Ecuador) as the original ones. 2) Based on the MJN analysis, only two colonizing events from northern South America to Central America would be considered. In this case, G1 → G3 → G5 → G4, and G2, and the additional colonization with the introgression of *N. olivacea*. All other details would be identical to the previous hypothesis. Other species of Neotropical mammals have also shown at least two colonization events from South America to Central America. An example is the case of the howler monkey (*Alouatta*; Ruiz-García *et al.* 2017), armadillo (*Dasypus novemcinctus*; Arteaga *et al.* 2012), or anteater (*Tamandua* sp.; Ruiz-García *et al.* 2021c). Using mitogenomic data, an alternative hypothesis can be proposed: 3) An *N. nasua* haplogroup in northern South America (Ruiz-Garcia *et al.* 2021a) gave rise to intermediate haplotypes between the current *N. nasua* haplotypes and the current *N. narica* haplotypes, some of which could still be detectable in southern Central America (southern Costa Rica). However, the haplotypes from the Central American *N. narica* would have originated in the north of present-day Colombia, as evidenced by the specimen of the PN Tama (North of Santander), which → MG1 (trans-Andean Ecuador) → MG3 → MG2, MG4, and MG5. In addition, the colonization of specimens introgressed with the mtDNA of *N. olivacea* (MG6) would have occurred. Therefore, this hypothesis proposes two colonizing events from South America to Central America, adding the possibility of a small colonizing event of intermediate haplotypes and even of haplotypes closer to *N. nasua* that occurred before the two major colonization events.

Ruiz-García *et al.* (2021a) proposed the beginning of mitochondrial evolution of the genus *Nasua* (including *Nasuella*) in the Andean zone of northwest South America 13–10 Ma (Miocene). This is consistent with the start of an intense uplifting in the central and northern Andes estimated to have occurred between 13 and 11 Mya (Antonelli *et al.* 2009; Hoorn *et al.* 2010) and with the completion of the Pebas system, which was characterized by the complete, or almost complete, flooding of the western Amazon during the Middle Miocene (Hoorn *et al.* 2010). From 11 to 7 Mya, another rapid uplifting of the Andean zone took place (Quechua II and III phases; Noble *et al.* 1990; Antonelli *et al.* 2009), and the Pebas System was replaced by the Acre fluvial system (Hoorn *et al.* 2010). These geomorphological and hydrological changes may have contributed to the emergence of different genetic clusters within *N. nasua* and the genesis of *N. olivacea.* However, this means that the ancestors of the current coatis had already reached South America during the Middle Miocene, supporting the hypothesis that the closure of the Central American Seaway occurred 15–13 Mya (Farris *et al.* 2011; Montes *et al.* 2012a b, 2015; Carrillo *et al.* 2015; Ruiz-García *et al.* 2018a).

According to the results reported here, the oldest *N. narica* haplotypes in South America seem to have emerged 4.5–3.2 Mya (Pliocene), with the Andes having played a major role. During the Pliocene, the eastern Andes mountain range in Colombia did not reach 40 % of their current elevation (Hoorn *et al.* 2010). The uplifting of the Andes continued until 2.7 Mya (Andriessen *et al.* 1994; Gregory-Wodzicki 2000). Therefore, the Andes mountain range itself may have been a physical and climatic barrier for multiple

species that previously would have been widely distributed in northwestern South America (Miller *et al.* 2008; Rull 2011). This period was characterized by glaciations in Argentina (3.5 Mya; Mercer 1984), Bolivia (3.27 Mya; Clapperton 1981), Chile (3–2 Mya; Caviedes and Paskoff 1975). According to the standard GABI model, the Isthmus of Panama emerged completely around 3.5–3.0 Mya (Middle Pliocene) with the definitive closure of the Central American Seaway (Coates and Stallard 2013; O'Dea *et al.* 2016), which could enable some colonizing events by *N. narica* from South America to Central America. Therefore, the case of coatis is contrary to the hypothesis supported by the fossil record, which suggests the predominance of a north-to-south colonization process that occurred 2.8–2.4 Mya (Simpson 1980; Webb 2006; Woodburne 2010). However, the Central American Seaway closure model during the Middle Miocene (15–13 Mya) seems more likely as it predicts active colonization from South America to North America over the past 6 Mya (Bacon *et al.* 2015; Marko *et al.* 2015), as observed for the coati in the present study.

The formation of the truly Central American haplotypes (excluding those of G6-MG6) took place between 1.9-1.1 Mya (Pleistocene), but the time of the introgression of *N. olivacea* into an *N. narica* group also occurred in this period (2.3–0.8 Mya). Nigenda-Morales *et al.* (2019) placed the divergence of the Central American groups at around 1.3 Mya, within the time range established in the present study. During this period, particularly in the range of 1.3–0.8 Mya, called Pre-Pastonian (maximum glacial peak of the great Gunz glaciation), the Central American groups of *N. narica* started to emerge. This period was extremely dry, which significantly reduced the extent of forests and boosted much of the genetic structure in different species of Neotropical mammals (*Lagothrix* sp., Ruiz-García *et al.* 2014, 2019a, 2020b; *Puma yagouroundi*, Ruiz-García *et al.* 2018b; *Lycalopex* sp., Ruiz-García *et al.* 2013).

The genetic structuring of *N. narica* in Central America during the Pleistocene is consistent with the refuge hypothesis (RH; Haffer 1969, 1997, 2008; Vanzolini 1970; Vanzolini and Williams 1970) of alternating humid-dry periods as a result of the Milankovitch cycles. This led to periods of forest contraction where much of the fauna was relegated. During dry periods, forests became shelter patches isolated by shrub zones, savannas, or arid steppes. This fostered the divergence between populations of the same species that became isolated in different refuges and the emergence of new lineages within them. Conversely, forests expanded in the humid periods, and the different lineages coexisted again in sympatric territories. At that time (1.30–1.10 Mya), sixth and seventh North American glaciations occurred (1.1–0.9 Mya) that affected southern México and northern Guatemala (Barendregt and Duk-Rodkin 2011; Rutter *et al.* 2012) and could have led to the differentiation of the G3 haplotypes from G4 and G5. Subsequently, the Reid glaciation (0.3–0.13 Mya; Barendregt and Duk-Rodkin 2011; Rutter *et al.* 2012), with severe dry peaks in North and Central America (Dansgaard *et al.* 1993; Hodell *et al.* 2008), also significantly reduced the extension of forests in Central and North America where *N. narica* lived, leading to the diversification within groups G3 and G5.

In Central America, more recent divergence processes have already occurred. For instance, the MJN showed that G5 (MG5) may have produced G4 (MG4) about 0.12–0.09 Mya. Although Hooghiemstra (1984) defined up to 27 potential climate changes with a periodicity of 100,000 years in the Colombian Andes (which also may had been reflected in Central America), there is only definitive evidence of the start of a great glaciation 116,000 years ago (Van der Hammen and González 1963; Van der Hammen *et al.* 1981; Helmens 1988; Florez 1992).

Genetic diversity and spatial structure. The levels of mitochondrial genetic diversity of *N. narica* were high but lower than those estimated for *N. nasua*, *N. olivacea*, or *P. flavus* (Ruiz-García *et al.* 2019b, 2020a, 2021a). This is correlated with the more recent origin of the ancestor of *N. narica*. In general, the populations that emerged more recently and peripheral to their geographic range have lower genetic diversity levels. The populations of other mammal species distributed in South America and which later colonized Central America and the south of the USA have lower genetic diversity levels than South American populations (long-nosed armadillo, *Dasypus novemcinctus*, Huchon *et al.* 1999; Arteaga *et al.* 2012; puma, *Puma concolor*, Culver *et al.* 2000; jaguarundi, *Puma yagouroundi*, Holbrook *et al.* 2013; Ruiz-García *et al.* 2018b).

In addition, a geographic pattern is observed in the distribution of genetic diversity. The groups living in northwestern South America (G1), and the southernmost part of Central America, introgressed by *N. olivacea* (G6), have the highest genetic diversities, whereas the northernmost groups of Central America have lower genetic diversity values. The group of Yucatán (México; G2) is an exception.

The spatial structure of *N. narica* was conspicuous and widespread throughout its range (Silva-Caballero *et al.* 2017, Nigenda-Morales *et al.* 2019), which appears to be common in the procionids studied from a population genetics stsandpoint (*e. g., N. nasua*, *N. olivacea*, or *P. flavus*; Ruiz-García *et al.* 2019b, 2020a, 2021a). In addition to the philopatric behavior of coati females and the climatic and ecological changes already described, geographic barriers may also have been drivers of the high spatial structure found in *N. narica*. Three physical barriers would help understand the spatial structure found in this study. The area between the Sierra Madre Oriental and the Isthmus of Tehuantepec south to the Nicaraguan depression is home to the groups G5, G2, G4, and part of the specimens of G3. In the area between the Nicaraguan depression and the Talamanca Mountain range (southern Costa Rica and northern Panama, whose emergence is dated at 5–3 Mya; MacMillan *et al.* 2006; Mann *et al.* 2007), we found another part of the specimens of G3 and one specimen of G6. In the area between the Talamanca Mountain range and the Darien

region, we found the introgressed specimens of G6. Some of these barriers emerged at times consistent with the estimated divergence times between the *N. narica* groups and have been effective geographic barriers for different taxa. The Talamanca Mountain range has been a geographic barrier for reptiles (Daza *et al.* 2010) and mammals (Bradley *et al.* 2008; Harding and Dragoo 2012; Hardy *et al.* 2013). The same is true for the Nicaraguan depression, characterized by marine transgressions during the Pliocene and Pleistocene (Bagley and Johnson 2014), which have been effective in isolating rodent species (Gutiérrez-García and Vázquez-Domínguez 2012). The territory delimited between the Motagua-Polochic-Jocotan fault (southern Guatemala) and the Isthmus of Tehuantepec (México) has been considered an area of endemic fauna delimited by these geographic barriers (Daza *et al.* 2010; Gutiérrez-García and Vázquez-Domínguez 2013), although this area originated 6–3 Mya, that is, before the arrival of *N. narica* to that area of Central America.

However, these physical barriers only partially explain the groups found in this study. Within the first area delimited by the physical barriers just mentioned (Sierra Madre Oriental and the Isthmus of Tehuantepec south to the Nicaraguan depression), we defined three groups that, in principle, are not separated by physical barriers, and we even found specimens of G3, *i. e.*, the only group found in the second geographic area delimited by the geographic barriers mentioned above (between the Nicaraguan depression and the Talamanca mountain range). The G6 specimens were found basically in the third geographic area mentioned (between the Talamanca mountain range and the Darien region); however, one specimen was found on the other slope of the Talamanca mountain range, whereas the Colombian specimens of the same group were found on the other side of the Darien region. Therefore, we consider that the behavior of the species and climatic changes were more relevant for defining the spatial structuring of *N. narica* than orographic barriers.

Our findings based on mtDNA can be interpreted as a first step toward solving the issue regarding the systematics of *N. narica*. This study provides the most comprehensive mitochondrial analysis and includes the widest geographic range covered to date for the species. However, the study of nuclear markers is essential to determine the hybridization and gene flow levels between the different mitochondrial groups of *N. narica* and achieve a complete evolutionary understanding of this species. Similarly, sampling efforts should be expanded to better understand the origin of this species.

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