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ORIGINAL ARTICLE

Historical climate change as driver of populational range expansion and differentiation in a rare and partially migratory Neotropical bird

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Abstract

Populations peripheral to a species' distribution are more susceptible to new selective pressures, changes, differentiation, and extinction. The Sooty Swift *Cypseloides fumigatus* (Apodidae) is a rare bird found mainly in central and southeastern South America. Populations of this species are resident in some localities throughout the year, whereas other populations migrate following the breeding season. Recently, a northern population was found well beyond the limits of its known distribution, with approximately 1000 km of occurrence gap between this newly discovered population and the southern distribution. Here, we reveal changes in species distribution over time, as well as compare the morphometric and genetic patterns of populations in the central-southern distribution of the Atlantic Forest and the northern peripheral population within the Caatinga. Our climate niche models indicate a scenario of expanding species distribution during the Last Glacial Maximum, which potentially drove the colonization of the northernmost population. This scenario of peripheral isolation is also supported by the spatial morphometric and genetic variation among populations of the humid forest enclave within the Caatinga and the Cerrado–Atlantic Forest populations. These findings provide important insights into the connectivity between distant Sooty Swift populations, the species' migratory behavior, as well as implications for conservation.

Keywords Apodidae · Atlantic forest · Ecological niche model · Founder effect · Morphological variation · Swift

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Zusammenfassung

Historischer Klimawandel als Auslöser für Ausbreitung und Auftrennung einer seltenen, teilziehenden neotropischen Vogelart

Populationen aus den Randbereichen des Verbreitungsgebiets einer Art sind empfindlicher gegenüber neuen Selektionsdrücken, Veränderungen, Differenzierung und Aussterben. Der Rauchsegler *Cypseloides fumigatus* (Apodidae) ist ein seltener Vogel, der hauptsächlich im zentralen und südöstlichen Südamerika vorkommt. Populationen dieser Art sind mancherorts Standvögel, während andere im Anschluss an die Brutsaison abwandern. Kürzlich wurde eine nördliche Population deutlich außerhalb der Grenzen des bisher bekannten Verbreitungsgebiets entdeckt, die durch eine Verbreitungslücke von etwa 1.000 km vom südlichen Areal der Art getrennt ist. Wir zeigen zeitliche Veränderungen der Artverbreitung und vergleichen morphometrische und genetische Muster in Populationen des zentral-südlichen Verbreitungsgebiets im Atlantischen Regenwald und in der nördlichen, peripheren Population innerhalb de Caatinga. Unsere Klima-Nischenmodelle weisen auf ein Szenario mit einer Ausweitung des Verbreitungsgebiets der Art auf dem Höhepunkt der letzten Eiszeit hin, die möglicherweise die Kolonisierung der am weitesten nördlich gelegenen Population vorangetrieben hat. Dieses Szenario einer peripheren Isolation wird auch durch die räumliche morphometrische und genetische Variabilität zwischen Populationen der feuchten Wald-Enklave innerhalb der Caatinga und den Cerrado/Atlantischer Regenwald-Populationen gestützt. Aus diesen Ergebnisse leiten sich wichtige Erkenntnisse über die möglichen Verbindungen zwischen entfernten Rauchsegler-Populationen, über das Wanderverhalten der Art sowie ihren Schutz.

Introduction

Historical climate changes often drive species range expansion, which may expose the new founding populations to different demographic and adaptive conditions. In these cases, peripheral differentiation might be an expected evolutionary consequence (Bell et al. 2010; Castellanos-Morales et al. 2016). As peripheral populations are typically smaller than central ones, they would be expected to present low phenotypic and genetic variability. This is because peripheral populations tend to be more susceptible to selective pressures and genetic drift, which may accelerate the divergence process (Lesica and Allendorf 1995; Petren et al. 2005).

The shift in selective pressure is an important characteristic of peripheral populations, which may be significantly different from those of the core population (Lawson et al. 2015). In fact, peripheral populations would be expected to change gradually from the typical niche of the species, with increasing geographic distance from the core population (Frey 1993; Hoskin et al. 2011). Under suitable environmental conditions, marginal populations may occur in habitats that are atypical for the species, which may drive both phenotypic and genetic differentiation resulting from divergent selective pressures (Edwards et al. 2005; Sinai et al. 2019).

Also, peripheral populations will be expected to have lower genetic variability than more central ones, due to the successive extirpation of low-frequency alleles through demographic events (e.g., bottlenecks), and reduced gene flow with the central, or core population, which will decline with increasing geographic distance (Petren et al. 2005; Lawson et al. 2015). These processes may be exacerbated by environmental degradation and natural disasters, which fragment habitats and may cause the extinction of intermediate populations, reinforcing the need for conservation efforts that, in turn, require a reliable understanding of the level of differentiation of the populations and their evolutionary potential (Lesica and Allendorf 1995; Lawson et al. 2015).

The Sooty Swift, *Cypseloides fumigatus* (Aves: Apodidae), is broadly distributed in South America, although its geographic range is poorly defined, being based on a small number of widely scattered records (Stopiglia and Raposo 2007; Albano and Girão 2008; Pearman et al. 2010; Biancalana et al. 2012; Biancalana 2015). The aerial habits of this species tend to restrict observations and capture in periods other than the breeding season, which coincides with the onset of the rainy season at most localities (Stopiglia and Raposo 2007; Chantler and Driessens 2000; Biancalana 2015). One characteristic of the breeding behavior of the Sooty Swift is its preference for nesting sites located on cliffs and rockfaces adjacent to or behind the drops of small- to medium-sized waterfalls (Stopiglia and Raposo 2007; Vasconcelos et al. 2006; Pearman et al. 2010; Biancalana et al. 2012; Biancalana 2015). Some authors also consider this species to be partially migratory, given that some populations may abandon their nesting sites after the breeding season, while others (a much smaller proportion) appear to remain resident throughout the year (Vasconcelos et al. 2006; Stopiglia and Raposo 2007; Biancalana et al. 2012).

Some recent studies (Vasconcelos et al. 2006; Albano and Girão 2008; Biancalana et al. 2012) have recorded breeding populations of the Sooty Swift at localities in the Cerrado and Caatinga biomes of central and northeastern Brazil that are well outside the limits of the known distribution of the species (Fig. 1). The population found in the Caatinga, in the Serra do Baturité, a mountain range in the Brazilian state of Ceará, is the northernmost occurrence yet recorded for the species (Albano and Girão 2008). This natural discontinuity of the species' distribution between the Serra do

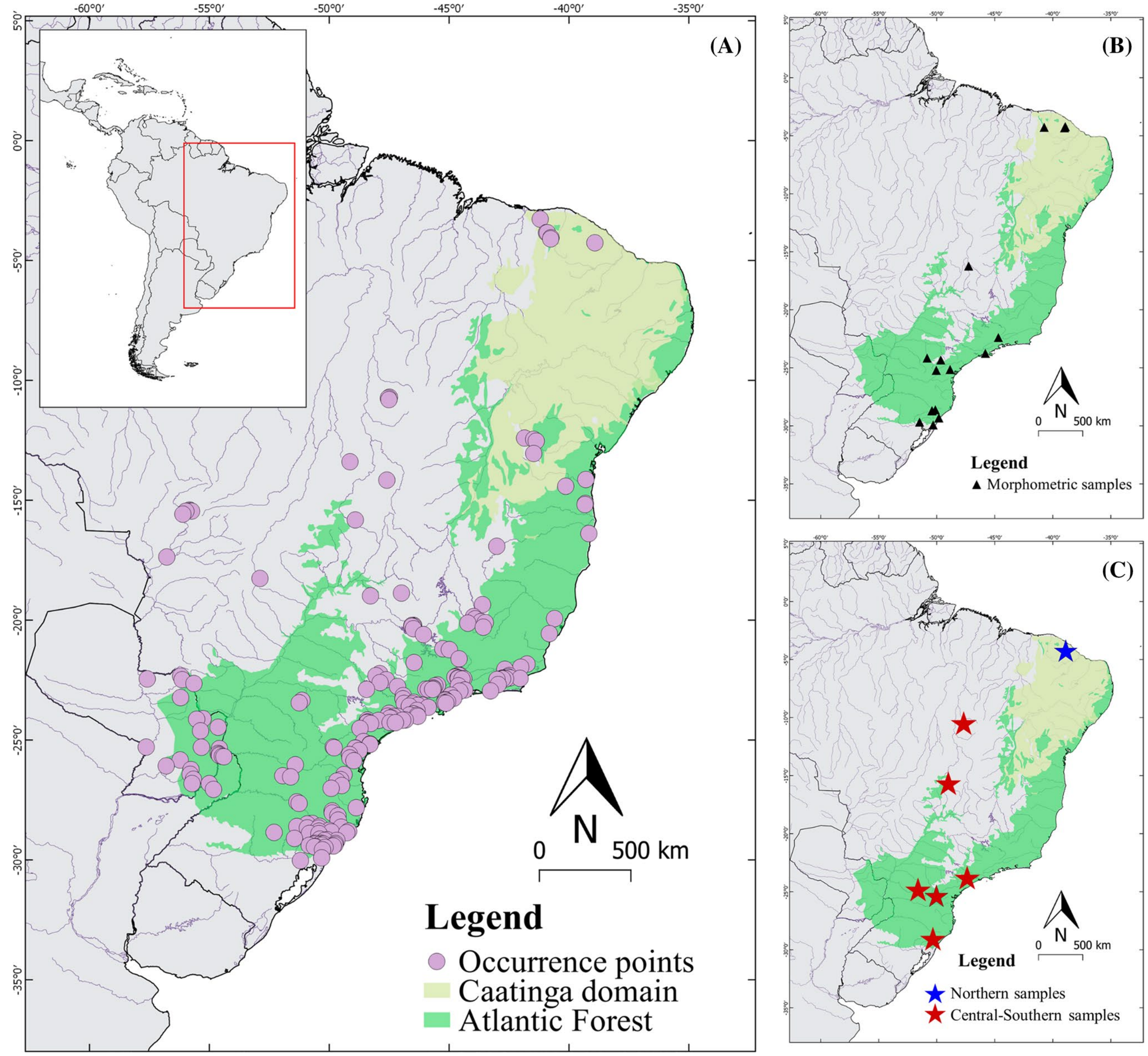

Fig. 1 Map of the Sooty Swift sampling records for **A** selected occurrences (213 locations) to build the climate niche models, mapped at a resolution of 5 km × 5 km distance between the locations; **B** locations of the skins samples used in morphometric analysis; **C** locations of the tissue samples used in genetic analyses: the northern Caatinga samples, in the Serra de Baturité (blue star) and the population of the central-southern Cerrado–Atlantic Forest samples (red star). The shaded polygons indicate the different forest domains found within the species' range, that is, the Atlantic Forest and the cloud forest enclaves (green) isolated within the Caatinga biome (light yellow)

Baturité and Chapada Diamantina (ca 1100 km apart), the previous northernmost locality of the species in the state of Bahia indicates that the Ceará population may be isolated in an enclave of cloud forest in the dry vegetation of the Caatinga. These humid forest enclaves are known locally as *brejos de altitude*, which refers to their occurrence at altitudes between 700 and 1200 m-asl. These environments are assumed to be relicts of a past connection between the Amazon and Atlantic Forest biomes, and are characterized by their considerable biological diversity and endemism (Souza and Oliveira 2006; Albano and Girão 2008; Silveira et al. 2019).

The diversity of endemic species in these cloud forests has been linked to peripatric speciation through the isolation of populations from neighboring biomes, such as the Amazon and Atlantic Forests, and the Cerrado of central Brazil (Carnaval 2002; d'Horta et al. 2013; Batalha-Filho et al. 2014; Luna et al. 2017; Silveira et al. 2019). The isolation of these populations probably resulted from the retraction of the forest corridors that formed across the Caatinga during periods of relatively humid climate, leading to the genetic and phenotypic differentiation of the relict populations (Carnaval and Bates 2007; Werneck 2011; Luna et al. 2017; Amaral et al. 2018). To the best of our knowledge, however, this isolation has only been observed in species with a low dispersal capacity, and not in organisms with the potential for long-range migrations.

Within this context, we evaluated changes in historical niche distribution, and pattern of morphometric and genetic diversity of Sooty Swift populations found in the humid forest enclaves of Serra de Baturité (Caatinga), in gallery forests of the Cerrado, and in the core population of the Atlantic Forest in southern Brazil. Specifically, we test (i) whether historical climatic changes determined the distribution and connectivity of the Caatinga and Cerrado–Atlantic Forest populations; and (ii) whether the peripheral Caatinga population is phenotypically and genetically different from the more continuous Cerrado–Atlantic Forest populations. To answer these issues, we used an integrative approach that included ecological niche models and the analysis of morphometric variation patterns, combined with a preliminary assessment of mtDNA genetic diversity.

Materials and methods

Ecological niche modeling

We constructed the distribution models for the Sooty Swift using the ecological niche modeling (ENM) technique. A total of 507 occurrence records were obtained through fieldwork, established databases, and publications (Online Supporting Information, Fig. S1). Spatial correlations were determined in SDMtoolbox (Brown 2014), which reduced the database to 213 localities (Fig. 1A). The occurrence records were mapped in a grid of cells with a resolution of 2.5 min of the arc (approximately 4.5 km × 4.5 km). We selected one point per grid cell and omitted all other repeated points, as well as the cells that contained the same environmental information. We used the bioclimatic data available at WorldClim 1.4 (Hijmans et al. 2005), which provides 19 environmental variables, for the present and the Mid-Holocene (ca. 6000 years ago), the Last Glacial Maximum (ca. 21,000 years ago), and the Last Interglacial (ca. 120,000 years ago). The Spearman correlation was used to avoid correlated climatic variables ($r < 0.7$, Online Supporting Information Table S1).

We used six different modeling algorithms to estimate the potential distribution of the Sooty Swift: (1) Bioclim (Nix 1986), (2) GLM (Guisan et al. 2002), (3) Domain (distance by Gower; Carpenter et al. 1993); (4) RandomForest (Liaw and Wiener 2002); (5) Maximum entropy—Maxent (Phillips and Dudik 2008), and (6) Support vector machine (SVM) (Tax and Duin 2004). All algorithms were run in R software (R Core Team 2021). The SVM algorithm was executed using the ksvm function of the [kernlab] package of the R platform (Karatzoglou et al. 2004), and Random Forest by the [randomForest] package. All other algorithms were executed in the [dismo] package of the R platform (Hijmans et al. 2015). Following an algorithm ensemble approach (Araújo and New 2007), the binary maps were concatenated to compute the frequency of presences predicted for each grid cell, yielding a single consensus map per climatic scenario (Present Day, Middle Holocene, Last Glacial Maximum, and Last Interglacial). We used the lowest fitness value of an occurrence record (i.e., < 0.49) as a cut-off threshold to calculate predicted binary maps (e.g., Jiménez-Valverde et al 2011; Peres et al 2015 and Sobral-Souza et al 2015). We obtained the final consensus map for each climatic scenario by calculating the frequency of each algorithm.

To calibrate the models based on presence-background observations (SVM and Maxent), background points were selected randomly from a grid of cells in South America used as input for the evaluation of the models. For each model, 20 replicates were generated, adjusted using a double partitioning criterion, i.e., 75% for training, and 25% for testing of the points were selected at random for each of the 20 replicates in each algorithm. To evaluate the models, we used the True Skill Statistic (TSS) whose values vary from − 1 to 1. Negative values and values close to zero indicate that the model's predictions are not significantly different from a randomly generated model, whereas models with values closer to 1 are considered to be very good. In general, models with TSS values of over 0.5 are considered acceptable (Allouche et al. 2006).

Ecological niche overlap

We used PCA-env, Schoener's *D* (Schoener 1968), and Warren's *I* (Warren et al. 2008) to quantify the niche overlap among the Sooty Swift populations, based on niche equivalence and similarity, run in the Ecospat R package (Broennimann et al. 2018). Schoener's *D* is based on direct measurements of the occurrence densities modeled in environmental space, while Warren's *I* is based on the modified Hellinger distance, used to compare two probability distributions. These two indices range from 0 (no similarity) to 1 (high similarity). We controlled for the effect of climate equivalence through a similarity test (Warren et al. 2008), which examines whether the niches of two populations with partial or non-overlapping distributions are more different than expected at random (Warren et al. 2008).

Morphometric analyses

We analyzed the morphometric parameters of 52 individuals obtained from several different ornithological collections and the inventories of independent expeditions (Online Supporting Information, Table S2). We measured the tarsus and exposed culmen of each specimen with a 15 cm Mitutoyo© caliper (0.05 mm precision), the wing and tail with a 15 and a 50 cm ornithological ruler and weighed the body mass of each individual with a 50 g Pesola© spring balance (0.25 g precision), and with a digital scale. We compared the body mass, and the length of the wing (flat), tail, tarsus, and exposed culmen between populations using the Student's *t* test. We also applied a Principal Components Analysis (PCA) of the different parameters to characterize the overall size variation among populations. We ran all these analyses in JMP® 10.0.0 (SAS Institute Inc. 2012).

Specimen sampling and DNA extraction

Due to the difficulty to obtain samples of the Sooty Swift out of the breeding season, we used samples available from some scientific collections to extract DNA. A total of 36 Sooty Swift samples were analyzed, 31 feather shaft samples were provided by the Associação de Pesquisa e Preservação de Ecossistemas Aquáticos (AQUASIS) and the Universidade Federal do Rio Grande do Norte (Online Supporting Information Table S3). Two blood samples and two tissue samples from different museum collections were obtained and processed by RNB (Online Supporting Information Table S3). We also used data available for the species on GenBank (NC_034933). Twenty of these samples were collected in the Atlantic Forest of southeastern Brazil, 18 in the Vila Velha State Park located in the municipality of Ponta Grossa, in the state of Paraná, one at the Parque Estadual Intervales, in the municipality of Ribeirão Grande, state of São Paulo, and one at Parque Eólico de Osório, in the municipality of Osório, Rio Grande do Sul. Two samples from the Cerrado were collected in the Parque Municipal Salto do Itiquira, in the municipality of Formosa, state of Goiás, and at the Cânyon da Sussuapara, in the municipality of Ponte Alta do Tocantins, state of Tocantins, while other 13 samples were collected from the population in the Serra de Baturité, in the municipality of Pacoti, in the northeastern state of Ceará (Fig. 1C).

Samples of feathers were stored in microtubes, in absolute ethanol (SISBIO/ICMBio authorization 19849-1). The DNA was extracted using the Wizard® Genomics DNA Purification kit (Promega), following the manufacturer's protocol. The mitochondrial genes NADH desidrogenase subunit 2 (ND2) and Cytochrome b (cytb) were amplified by Polymerase Chain Reaction (PCR) using the primers described by Sorenson et al. (1999) (list of primer sequences in the Online Supporting Information Table S4). Standard protocols and methods (Sambrook and Russell 1989) were used to obtain the sequences of these markers in an ABI 3500 XL automatic sequencer (Applied Biosystems).

Genetic diversity and population structure

The sequences were aligned using the automatic multiple alignment tool in ClustalW (Thompson et al. 1994) runs in BioEdit 7.2.0 (Hall 1999). The haplotype (Hd) and nucleotide (π) diversity of each population were estimated using DnaSP 6 (Rozas et al. 2017). The haplotype networks were plotted in Haploviewer (Salzburguer et al. 2011), using a maximum likelihood topology. Tajima's (1989) *D* and Fu's (1997) *F*s were also calculated to test for possible trends of historical demographic change. These tests were based on coalescent simulations of 1000 replicates, run in DnaSP 6.

The genetic structure of the Sooty Swift populations was determined using the Bayesian Analysis of Population Structure software (BAPS 6—Corander et al. 2008), considering the premise of non-spatially hierarchical genetic mixing at an individual level. Models testing for the presence of up to seven populations (*K*) were tested (relative to the number of sampled locations, Fig. 1C), with each search being replicated 100 times. Hierarchical analyses of molecular variance (AMOVA) and fixation indices (*F*st) were calculated in Arlequin 3.5 (Excoffier and Lischer 2010) for the two populations, from the Cerrado–Atlantic Forest (central-southern) and the Caatinga (northern). We also performed an exact test of population differentiation to test the non-random distribution of haplotypes in the sampled populations under the assumption of panmixia (for both individual and concatenated markers). The significance was evaluated by 1000 random permutations using Bonferroni's sequential correction.

Data availability

GenBank accession numbers for the mitochondrial marker sequences of Cytb (OL311723-OL311753) and ND2 (OL311754-OL311786) can be found in Supplementary Material file 1 Table S3. Occurrence data of *Cypseloides fumigatus* used in the analyses of niche modeling can be found in the Supplementary Material file 2 - Occurences_Cypseloides_fumigatus.xlsx. Data on morphometric measurements of *Cypseloides fumigatus* samples can be found in Supplementary Material file 3 - Cypseloides_fumigatus_morphometric_measures.xlsx

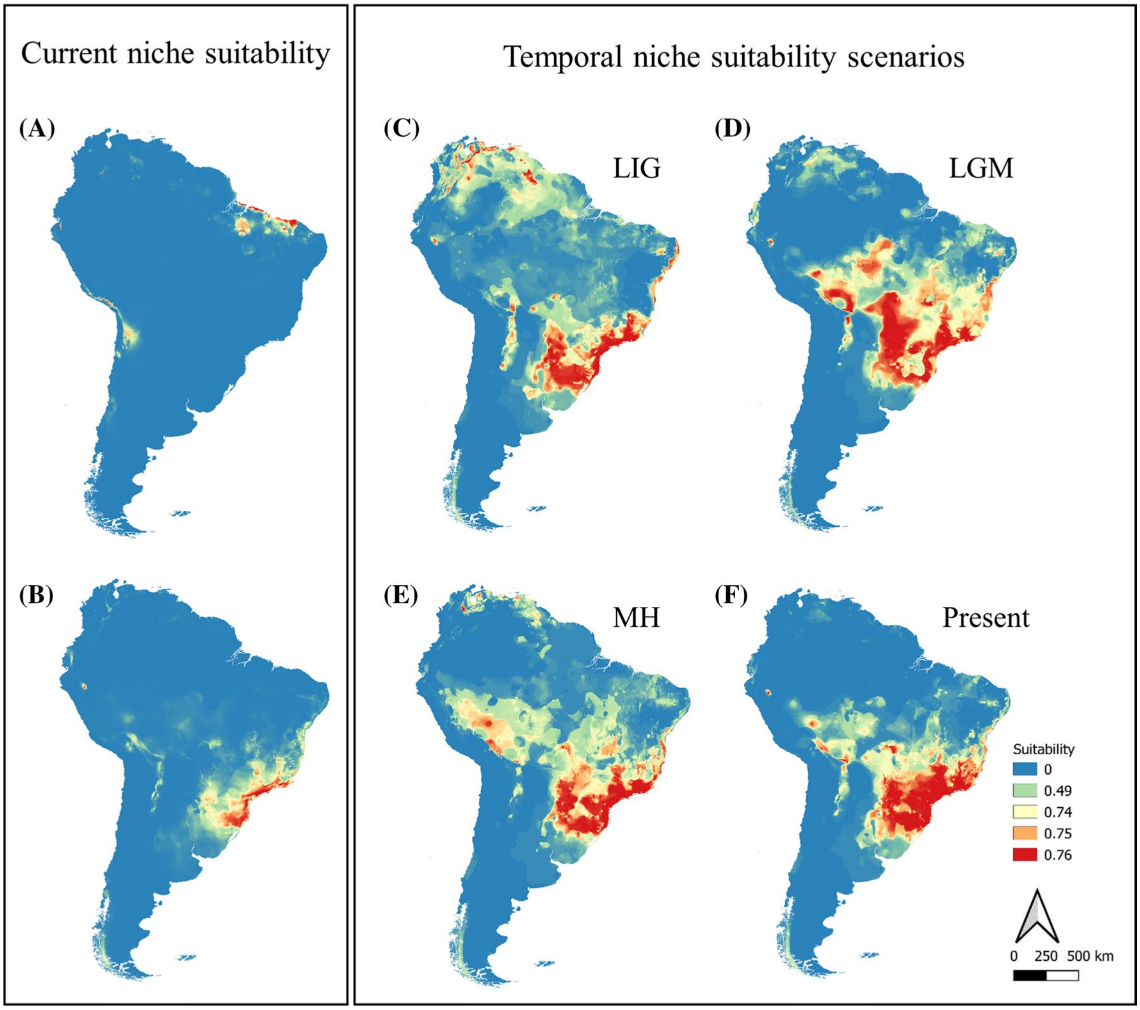

Fig. 2 Niche suitability models for current Sooty Swift populations from South America and under four different temporal climatic scenarios. **A** Model of the northern populations in the cloud forest enclaves in the Caatinga domain and **B** model for the central-southern population in the Cerrado and Atlantic Forest. Temporal climate scenario for **C** the Last Interglacial (ca 120,000 years ago), **B** Last Glacial Maximum (ca 22,000 years ago), **C** Mid-Holocene (ca 6000 years ago), **D** present-day conditions. The blue areas have sensitivity–specificity maximization values below the established threshold

Results

Niche modeling and overlapping

Evaluation of the six niche modeling algorithms showed AUC values > 0.8, indicating high model performance. (Online Supporting Information, Table S5). The present-day models created separately for the two populations revealed no overlap between them (Fig. 2A, B). The predictions of the temporal climate niche model indicates the expansion of the Sooty Swift population from the Last Interglacial (LIG 120,000 years) to Last Glacial Maximum (LGM 22,000 years), followed by a slight reduction during the Mid-Holocene (MH 6000 years) to the present (Fig. 2C–F).

The niche models generated for the two populations indicated differentiation due to the lack of shared niche suitability (Online Supporting Information, Fig. S3). The results of the niche overlap analysis revealed low values (Schoener's $D = 0.028$ and Warren's $I = 0.12$), reinforcing the existence of significant differences between the niches of the two populations. The PCA-env also indicates a low level of overlap of the environmental space between the two populations (Online Supporting Information, Fig. S4). The similarity and equivalence tests also presented low D values when comparing the southern population with the northern population.

Despite the low D values, tests of niche similarity and equivalence comparing the northern and south-central populations were not significantly different from the null model ($p > 0.34$), which assumes that the environmental differences between the populations are due to the lack of a shared area (the black arrow is in the same position as the bars—see

Table 1 Comparison of the morphometric parameters recorded from Sooty Swift specimens sampled in the northern (Caatinga) and central-southern (Cerrado–Atlantic Forest) populations

Population	Body mass (g)	Wing (mm)	Tail (mm)	Tarsus (mm)	Exposed culmen (mm)
Northern	40.9 ± 2.8 36.5–45.5 (15)	149.9 ± 2.1 146.5–153.5 (17)	47.6 ± 1.3 45.0–49.5 (17)	13.79 ± 0.31 13.30–14.35 (17)	6.05 ± 0.28 5.50–6.50 (17)
Central-Southern	40.0 ± 3.0 33.3–45.0 (30)	155.9 ± 4.1 140.0–164.0 (34)	49.5 ± 1.5 47.0–53.0 (35)	14.70 ± 0.72 13.50–15.75 (30)	6.04 ± 0.30 5.50–6.6 (29)
t	$t_{43} = 0.96, p = 0.34$	$t_{49} = 5.66, p < 0.01$*	$t_{50} = 4.63, p < 0.01$*	$t_{45} = 4.97, p < 0.01$*	$t_{44} = 0.10, p = 0.92$

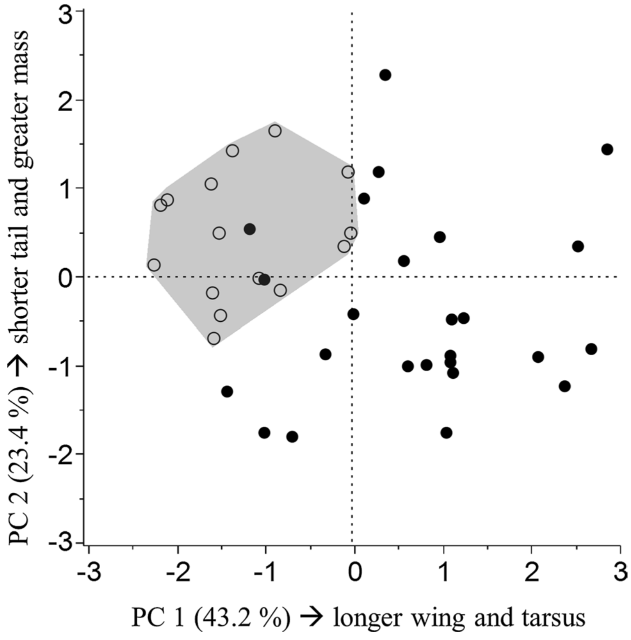

Fig. 3 Results of the Principal Components Analysis of the morphometric measurements of the Sooty Swift from Brazil. The open and solid circles represent specimens sampled in the northern and central-southern populations, respectively, while the gray polygon encompasses all the northern specimens plus two specimens from the central distribution (Minas Gerais) of the species. The analysis was based on the measurements of the wing, tail, tarsus, mass, and exposed culmen. Components 1 and 2 accounted for 43.2% and 23.4% of data variance (eigenvalues of 2.16 and 1.17), respectively

Online Supporting Information, Fig. S3). This interpretation should be viewed with caution, however, given that this difference between environments may be at least partly determined by the restricted geographic distribution of the northern population. When the number of records available after the rarefaction of the points is compared, only six points were recovered for the northern population, compared with 208 for the southern population.

Morphometry

The northern individuals presented mean wing, tail, and tarsus measurements significantly smaller than those of the central-southern individuals, although the mean body mass and exposed culmen did not vary significantly between populations (Table 1). In the Principal Component Analysis, PC 1 (wing and tarsus length) and PC2 (tail length and mass) explained 43.2% (eigenvalue = 2.16) and 23.4% (eigenvalue = 1.17) of the variance in the data, respectively. The scatter plot of the principal components indicated only a slight separation between individuals from the northern and central-southern populations. However, two specimens from the state of Minas Gerais were closer to the northern population (Fig. 3).

Genetic diversity and population structure

A total of 1328 base pairs (bp) of the mitochondrial genome were sequenced, specifically 938 bp from ND2 and 390 bp from Cytb (Table 2). The two populations analyzed here presented distinct levels of genetic variability (Table 2), with the Caatinga (northern) population presenting Hd and π values of zero, while the Cerrado–Atlantic Forest (central-southern) population presented moderate levels of diversity (ND2–Hd = 0.668 and $\pi = 0.0011$; cytb = 0.587 and 0.0020). The northern population presented a single haplotype (H1) for both markers, whereas the central-southern population presented twelve haplotypes (ND2 = 5; cytb = 7). In both cases, H1 was the most frequent haplotype, and the only one shared between the two populations (Fig. 4A). The absence of variability in the northern population impeded any analysis of deviations from neutrality. The central-southern population presented negative and significant deviations from neutrality ($D = -0.6860$; $Fs = -2.692$ $p > 0.1$ for the concatenated markers), indicating selective sweep or population expansion after a recent bottleneck event.

The BAPS analysis of population structure indicated the existence of two groups ($K = 2$, marginal probability = − 172.8; Online Supporting Information, Table S6), with one group being present universally and the other being restricted to the central-southern region (Fig. 4B). By incorporating geographic locations explicitly in the definition of the genetic structure, the *F*st values were significant and corresponded to a population genetic structure ($F\text{st} = 0.191$, $p < 0.01$; Table 2). The *p*-distance value 0.001 suggests no structure between populations (Table 2), while the AMOVA

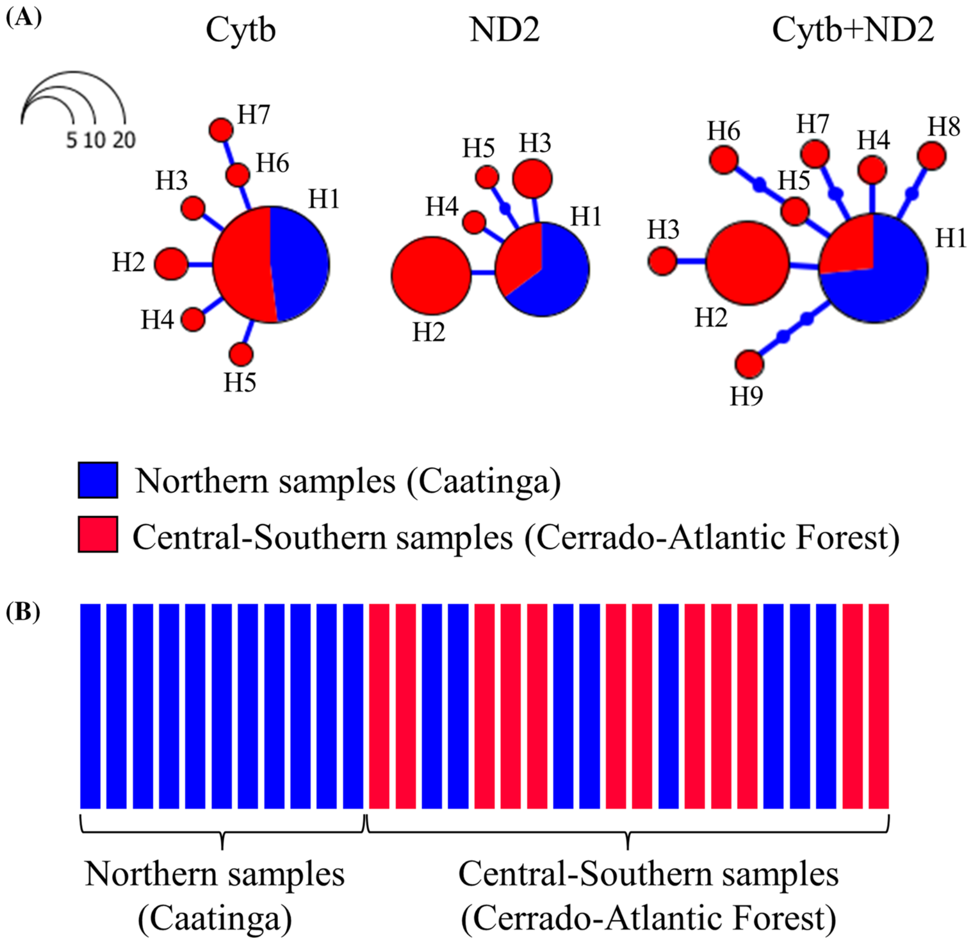

Fig. 4 Haplotype network based on the maximum likelihood analysis of the mtDNA markers Cytb, ND2, and both markers (Cytb + ND2) between the northern Caatinga domain (blue) and central-southern Cerrado–Atlantic Forest (red) samples

result indicates slight differentiation (Table 3), with most of the genetic variation being present within populations (80.83%) than among populations (19.16%). The exact test of population differentiation indicated that haplotypes are not randomly distributed among populations when evaluating concatenated mtDNA markers ($p < 0.001$), but the same was not true for individual markers ($p > 0.8$).

Discussion

Our results of niche distribution, morphometric and genetic variation support the peripheral differentiation of the Caatinga Sooty Swift population relative to the Cerrado–Atlantic Forest populations. The historical variation in species distribution (Fig. 2), along with morphometric differentiation (Fig. 3, Table 1) and lack of genetic diversity (Fig. 4, Table 2), support the hypothesis that the peripheral isolation of the Caatinga population could be driven by the founder effect due to climate change during the LIG (120,000 years) to LGM (21,000 years) transition. Furthermore, within the distribution of our samples, Sooty Swift showed low to moderate genetic diversity, with signs of recent population expansion in the Cerrado–Atlantic Forest region (Table 2). Below, we discuss how the patterns observed here provide some insights into the ecological, evolutionary, and vulnerability aspects of the rare and poorly known Sooty Swift.

Historical distribution shifts, morphometric and genetic patterns of the Sooty Swift

Paleoclimatic models developed for the Quaternary indicate greater stability in the distribution of forests in the core of the Atlantic Forest compared to its peripheral areas (Carnaval and Moritz 2008; Carnaval et al. 2009), which include the humid forest enclaves within the Caatinga domain (Cabanne et al. 2016). This shift in environmental distribution seems to have shaped the current species diversity through the cyclical effects of climate (Carnaval and Bates 2007; Batalha-Filho et al. 2013; Ledo and Colli 2017; Silveira et al. 2019). Our Sooty Swift ecological niche models suggest the possibility of a range expansion into the northeast from the south-central distribution during the LIG to the LGM, with possible connectivity through the northeast coastal Atlantic Forest (Fig. 2C, D), followed by a reduced niche range in peripheral northern areas during the middle

Table 2 Genetic summary on mitochondrial markers Cytb and ND2 (individual and concatenated) from Sooty Swift specimens sampled in the northern (Caatinga) and central-southern (Cerrado–Atlantic Forest) populations

Locus	Population	*N*	Length (bps)	*S*	*h*	Hd	π	Tajima's *D*	Fu's *F*s	*F*st	*P*-distance	
											Within	Between
ND2	Northern	11	938	0	1	0	0	NA	NA	0.1822*	0	0.001
	Central-Southern	23		5	5	0.668	0.0011	-0.7253^{ns}	-0.887^{ns}		0.001	
Cytb	Northern	12	390	0	1	0	0	NA	NA	0.127^{ns}	0	0.001
	Central-Southern	20		6	7	0.584	0.0020	− 1.7191*	− 5.515*		0.002	
ND2 + Cytb	Northern	11	1328	0	1	0	0	NA	NA	0.191*	0	0.001
	Central-Southern	20		11	9	0.779	0.0012	− 1.6020*	− 4.028*		0.001	

N number of samples; *bps* base pairs; *S* segregating sites; *h* number of haplotypes; *Hd* haplotype diversity; *π* nucleotide diversity; *Fst* fixation index

Holocene to present (Fig. 2E, F). Furthermore, these results also support the hypothesis of dynamic connectivity of habitat corridors between peripheral forest enclaves in northeastern (within the Caatinga domain) with central Atlantic Forest during past climate change (Carnaval and Bates 2007; Werneck 2011; Luna et al. 2017; Silveira et al. 2019).

For populations in the peripheral range, adaptive responses to new environmental conditions could drive rapid phenotypic differentiation and potential reproductive isolation (Grant and Grant 2011). Morphometric variation among bird populations is determined by selective pressures shifting along environmental gradients, which may exist throughout the entire geographic range of a species (Edwards et al. 2005). In this sense, the significant difference in morphometric measurements between the Sooty Swift populations sampled here could be the result of different selective pressures acting in their respective environments (Fig. 3, Table 1). This hypothesis is supported by the niche overlap results, which indicate differentiation due to the mismatch of shared niches as revealed by low values of Schoener's *D* (0.028) and Warren's *I* (0.12). These differences were mainly in the precipitation (Bio13, Bio15, Bio18, see Supplementary Material Fig. S3B), which is the environmental variable associated with the beginning of the Sooty Swift breeding season (Stopiglia and Raposo 2007; Chantler and Driessens 2000; Biancalana 2015).

In migratory birds, varying niche conditions across the species' distribution can result in changes in breeding schedules and potential allochronic isolation (see Taylor and Friesen 2017). For Sooty Swift populations in the Atlantic Forest, the trigger of migration to breeding sites is timed by the rainy season, which can range from September to March (Vasconcelos et al. 2006). In the Caatinga biome, rainy seasons are comparatively short and generally range from January to May. This dyssynchrony of rainy seasons across biomes may result in changes in the reproductive cycles of the peripheral Caatinga population, isolating it from other Atlantic Forest (or even from Cerrado) populations. Indeed, isothermality (Bio03) and seasonality of precipitation (Bio15) are among the environmental variables that contribute most to niche differentiation between northern and central-southern populations in our ecological niche models (Online Supporting Information Fig. S2).

Table 3 Results of the Analysis of Molecular Variance (AMOVA) for the concatenated mtDNA markers, within and among the northern and central-southern Sooty Swift samples analyzed in the present study

Source of variation	Sum of squares	Components of the variance	% Variation
Among population	2.432	0.1321	19.16
Within population	16.150	0.5569	80.83
Total	18.581	0.6889	

Allochronic isolation due to environmental changes within the species' range can lead to the loss of migratory behavior in favor of sedentary behavior (Taylor and Friesen 2017; Gómez-Bahamón et al. 2020). Losses in migratory behavior (i.e., migratory drop-offs) are often accompanied by changes in morphological traits (Hedenström 2008; Freedman et al. 2020). In our morphometric data, the significant reduction in wing, tail, and tarsus size of the Caatinga population samples compared to the Atlantic Forest and Cerrado may be the result of a loss of migratory behavior (Table 1). Especially with respect to wing size, which is a morphological trait closely associated with flight performance and ability (Savile 1957; Claramunt 2021), and it is possible that a reduction in these traits could also reduce migratory efficiency. If proven, this may be the first record of loss of migratory behavior recorded within a Neotropical Swift species.

Alternatively, morphometric divergence may be significant in small founder populations, indicating the influence of neutral processes such as drift that can drive rapid changes in phenotypic traits (Spurgin et al. 2014). According to this hypothesis, the observed morphometric differences between the central-southern and northern peripheral populations occur by chance due to founder effects, but not due to selective pressures. Evidence supporting this hypothesis is the ecological niche model indicating an increased species niche suitability in a northward direction, towards the Caatinga during the LIG–LGM transition (Fig. 2), and the low genetic (Fig. 4, Table 2) and morphometric (Fig. 2, Table 1) diversity of this population, which represents only a subset of the variation found in south-central populations (Table 3, Fig. 4). Furthermore, the exact test for population differentiation suggests that the distribution of haplotypes for the concatenated mtDNA markers is not random under the panmixia model, indicating that the possibility of a founder effect cannot be ruled out. This recent founder effect during the LGM to Mid-Holocene transect (21,000–6000 years), with subsequent extirpation of low-frequency haplotypes due to drift in a small population, could also explain the low genetic differentiation among populations (Table 3, Fig. 4). Despite these findings, it will be necessary to collect morphometric and genetic data from additional Sooty Swift populations in eastern and central Brazil to provide more conclusive insight into the process that drove the spatial variation found in this species.

Conservation implications

The Atlantic Forest and Caatinga biomes have the largest number of endemic and endangered species of any South American ecosystem (Leal et al. 2005; Tabarelli et al. 2010; Santos et al. 2011; Silva et al. 2017). This appears to be consistent with the low genetic diversity (Hd = 0; $\pi = 0$—for both mtDNA markers) and morphometric differentiation (Fig. 3) found in the Sooty Swift individuals from Serra de Baturité. These results further reinforce the conclusion that the enclaves of cloud forest found in the Caatinga are priority areas for conservation because, while they do not constitute significant genetic reserves, they do protect a variety of endemic species and divergent populations (Carnaval 2002; Albano and Girão 2008; Santos et al. 2007; Luna et al. 2017; Silveira et al. 2019).

In addition, the accentuated fragmentation and discontinuity of these Atlantic Forest habitats (Ribeiro et al. 2009) are associated with low levels of genetic diversity, which can be intensified by genetic drift in small populations with reduced gene flow (Dixo et al. 2009; Haag et al. 2010). This pattern appears to be constantly revealed by genetic and demographic history studies in some bird lineages (d'Horta et al. 2011; Batalha-Filho et al. 2012) and corroborated by our results of genetic variability estimated for the Atlantic Forest population of the Sooty Swift (Table 2).

A recent study of Sooty Swift populations in southeastern and central Brazil revealed a low degree of polymorphism in microsatellite markers, which may have been the result of behavioral and ecological factors, variation in population size, or, possibly, inbreeding (Biancalana et al. 2019). This is probably because pairs are highly philopatric and return to the same nests in successive breeding seasons, as observed in other swift species (Hirshman et al. 2007; Pichorim et al. 2009; Collins 2010; Pichorim and Monteiro-Filho 2010; Marín 2016). These characteristics are typical of birds with a high dispersal capacity, such as albatrosses and crows (Milot et al. 2007; Morinha et al. 2017). However, the lack of data on the ecology and natural history of species such as the Sooty Swift limit our ability to understand which factors may influence the observed patterns of genetic diversity. Understanding these characteristics is crucial to the development of effective conservation strategies that combine data on genetic and functional variability, to maintain the adaptive potential of the species (Harrison et al. 2014; Hoelzel et al. 2019).

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