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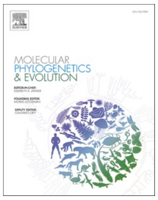

Comparative phylogeographic and demographic analyses reveal a congruent pattern of sister relationships between bird populations of the northern and south-central Atlantic Forest

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ABSTRACT

The Pernambuco Center of Endemism (PCE) is the northernmost strip of the Atlantic Forest (AF). Biogeographic affinities among avifaunas in the PCE, the southern-central Atlantic Forest (SCAF), and Amazonia (AM) have not been studied comprehensively, and current patterns of genetic diversity in the PCE remain unclear. The interplay between species' ecological attributes and historical processes, such as Pleistocene climate fluctuations or the appearance of rivers, may have affected population genetic structures in the PCE. Moreover, the role of past connections between the PCE and AM and the elevational distribution of species in assembling the PCE avifauna remain untested. Here, we investigated the biogeographic history of seven taxa endemic to the PCE within a comparative phylogeographic framework based on a mean of 3,618 independent single nucleotide polymorphisms (SNPs) extracted from flanking regions of ultraconserved elements (UCEs) and one mitochondrial gene. We found that PCE populations were more closely related to SCAF populations than they were to those in AM, regardless of their elevational range, with divergence times placed during the Mid-Pleistocene. These splits were consistent with a pattern of allopatric divergence with gene flow until the upper Pleistocene and no signal of rapid changes in population sizes. Our results support the existence of a Pleistocene refugium driving current genetic diversity in the PCE, thereby rejecting the role of the São Francisco River as a primary barrier for population divergence. Additionally, we found that connections with Amazonia also played a significant role in assembling the PCE avifauna through subsequent migration events.

1. Introduction

Neotropical forests are widely known for their high levels of species richness and endemism, and identifying the processes that generate and maintain this pattern is a challenging yet important goal in biogeography (Haffer, 1969; Hoorn et al., 2010; Ribas et al., 2012; Smith et al., 2014b). The Atlantic Forest (AF) is a Neotropical forest biome located along the eastern coast of South America from eastern Paraguay and northeastern Argentina to northeastern Brazil, and it is among the regions with the highest species richness on Earth (Mittermeier et al., 2005; Myers et al., 2000). Within the Atlantic Forest, the Pernambuco Center of Endemism is located north of the São Fransico river in the states of Alagoas, Pernambuco, Paraíba, and Rio Grande do Norte (Silva et al., 2004; Fig. 1), and it is recognized as an important area of endemism for plants (Prance, 1982), butterflies (Brown, 1979; Tyler et al., 1994), and birds (Silva et al., 2004; Tabarelli et al., 2010). Biogeographic relationships between the PCE, the rest of the Atlantic Forest (hereafter southern-central Atlantic Forest or SCAF), and Amazonia (AM) have hardly been addressed in recent studies (Santos et al., 2007) and unraveling the evolutionary mechanisms that account for the origin of the PCE's unique biological diversity is especially relevant to understand the origins and evolution of this biota.

The biota of the PCE is sometimes associated with higher elevation "islands" of humid forests in the Caatinga, known as *brejos de altitude* (Brown, 1982; Prance, 1982; Silveira et al., 2003; Tabarelli et al., 2006) and we follow Silveira et al. (2003) in including the *brejos de altitude* located in the states of Pernambuco and Paraiba, but not those in Ceará, as part of the PCE. In addition to having a unique biota, the PCE is

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considered the most threatened area of the AF, and it has been regarded as the most endangered region of the Americas (Pereira et al., 2014; Silva et al., 2004; Silveira et al., 2003; Tabarelli et al., 2010, 2006). At the onset of the 21st century, it was estimated that only 2% (1,907 km^2) of its original forest cover (39,567 km^2) remained (Silveira et al., 2003), mostly in small fragments isolated and surrounded by sugarcane plantations, and threatened by selective logging, poaching, and uncontrolled fires (Ranta and Blom, 1998; Silva et al., 2002; Silva and Tabarelli, 2001, 2000; Silveira et al., 2003; Tabarelli and Roda, 2005).

Including the *brejos de altitude*, the PCE currently harbors 435 species of birds, 18 of which are endemic to the PCE, and 21 of which have a subspecies endemic to the PCE (Barnett and Buzzetti, 2014; Batalha-Filho et al., 2013b; Pereira et al., 2014; Rêgo et al., 2014; Roda et al., 2011; Silveira et al., 2004, 2003). Because of the extensive deforestation described above and the observation that 65% of bird species are associated with forested environments (Roda et al., 2011), 15 species of bird occurring in the PCE are listed as endangered on the IUCN red list (IUCN, 2019), and four are considered extinct (IUCN, 2019; Pereira et al., 2014; Silveira et al., 2004). These numbers make the PCE the Neotropical region with the highest relative and absolute numbers of threatened and extinct bird species and perhaps many more could have gone extinct, even before being described (Lees et al., 2015; Olmos, 2005; Pereira et al., 2014; Silveira et al., 2003). In light of the region's dire conservation status, unraveling the processes that account for the origin and accumulation of the PCE's biological diversity is not only relevant to understand the evolution of this unique biota but also to provide a solid baseline for effective conservation in the region by defining which endemic taxa represent independent evolutionary lineages (Maldonado-Coelho, 2012; Richardson and Whittaker, 2010).

A wealth of hypotheses about the origin and maintenance of Neotropical diversity can potentially explain the mechanistic underpinnings of the composition of the PCE avifauna. These hypotheses mostly pertain to a) climatic oscillations that generated widespread contractions and expansions of forested environments (The Pleistocene Forest Refugia Hypothesis – PFR; Haffer, 1997, 1969); b) the formation of rivers that split species' ranges (Riverine Barrier Hypothesis – RB; Sick, 1967; Wallace, 1852), and c) past connections between distinct biogeographic regions. The PFR suggests that forest organisms were isolated in forest patches surrounded by open areas during glacial maxima. Cycles of forest fragmentation and reconnection resulted in high levels of species richness due to isolation through glacial periods and secondary contact between formerly isolated populations during interglacial times (Haffer, 1969; Vanzolini and Williams, 1970). Derived from the PFR, the stability-extinction model (Carnaval et al., 2009; Carnaval and Moritz, 2008) suggests that current patterns of intraspecific genetic variation are the result of periodic isolations in areas of forest stability (i.e., forest refugia) and extinction in areas outside refugia during the Last Glacial Maximum (LGM). It predicts the existence of two historically stable areas in the AF during the LGM, namely the Bahia and the Pernambuco refugia, of which the latter is coincident with the PCE. Thus, the avifauna of these refugia would be predicted to have stable demographic histories and high genetic diversity. In contrast, populations south of the Doce River (i.e., southern AF) would exhibit signatures of recent recolonization events from northern populations and a less stable demographic history (Carnaval and Moritz, 2008).

Although some studies have found stable areas corresponding to the proposed refugia (Amaral et al., 2013; Batalha-Filho and Miyaki, 2016;

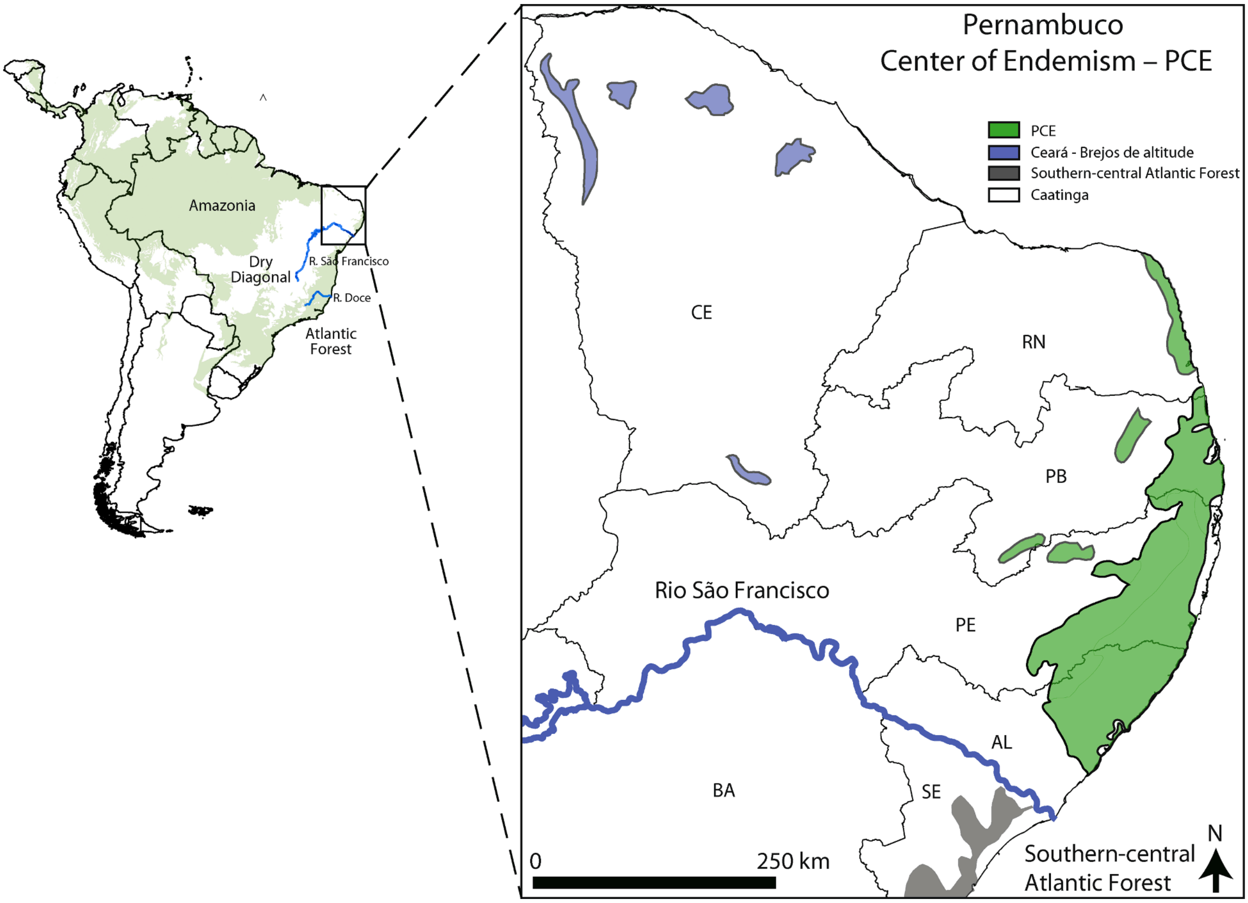

Fig. 1. Map showing the location of the Pernambuco Center of Endemism (PCE) in northeastern Brazil. The PCE corresponds to the forested area north of São Francisco River, including isolated enclaves of humid forest at higher elevations ("*brejos de altitude*"). Acronyms denote Brazilian states.

Bolívar-Leguizamón et al., 2020; Brunes et al., 2010; Carnaval et al., 2009; Dhorta et al., 2011; Fitzpatrick et al., 2009; Mata et al., 2009), others seem to contradict the stability extinction model (e.g., Alvarez-Presas et al., 2014; Amaral et al., 2013; Cabanne et al., 2008; Carnaval et al., 2009; Fitzpatrick et al., 2009; Thomé et al., 2010). For instance, using ecological niche models, Silveira et al. (2019) suggested that forests in the PCE expanded during the LGM into areas covered by present-day Caatinga, promoting connections between forested enclaves *(brejos de altitude*) that have only recently retracted to their current distribution. Based on species distribution models and molecular coalescent simulations of small mammals, Leite et al. (2016a,b) suggested that population expansions of the SCAF during the LGM followed the emergence of a continental shelf and lead them to propose that forest refugia have played a minor role in AF diversification. Likewise, palynological studies, geochemical studies, and distribution modeling of plant species from northeastern Brazil (Behling et al., 2000; Bouimetarhan et al., 2018; Dupont et al., 2010; Ledru et al., 2006; Oliveira et al., 1999; Pinaya et al., 2019) suggest that humid gallery forests expanded and contracted in areas now occupied by the Caatinga since the LGM until the end of the Pleistocene (~11 ka), followed by forest contraction to the present-day distribution during the Holocene. Together, these recent studies suggest that the PCE has a more dynamic and complex environmental history than previously proposed, in which other factors, besides the isolation in environmentally stable areas, could have shaped its diversification.

On the other hand, the RB hypothesis states that the origin of a river not only would create a barrier to gene flow but also would promote the initial differentiation of animals on opposite banks. Rivers and elevational zonations are generally associated with the distribution boundaries of many AF bird taxa. The Doce and São Francisco Rivers would be the most significant barriers as they delimit the main AF areas of endemism (Silva et al., 2004). The RB hypothesis dramatically differs from the PFR in its predictions. Specifically, genetic breaks between populations would match the rivers and not the limits of the proposed refugia, and the divergence times across species or populations pairs separated by the river would coincide with the timing of the river origin. Consequently, divergence times would be much older than predicted by the PFR, given that AF rivers are thought to predate the Pleistocene (Lundberg et al., 1998; Potter, 1997). Moreover, demographic fluctuations overtime should not be detected because cycles of extinction and expansion are not expected (Amaral et al., 2013; Maldonado-Coelho, 2012). Although several biogeographic studies of AF endemic taxa found that genetic breaks usually coincide with the boundaries of main rivers (Brunes et al., 2010; Cabanne et al., 2007; Lara-Ruiz et al., 2008; Pellegrino et al., 2005; Resende et al., 2010), their role as primary drivers of diversification in the AF remains controversial and lacks widespread support as is the case for Amazonian Rivers (Cracraft, 1985; Gascon et al., 1998; Haffer, 1997; Ribas et al., 2012). Furthermore, studies have provided evidence for recent population differentiation with signatures of demographic fluctuations, contradicting the expectations of the RB hypothesis (Batalha-filho et al., 2019; Bolívar-Leguizamón et al., 2020; Cabanne et al., 2008; Colombi et al., 2010; Maldonado-Coelho, 2012). An endemicity analysis of the PCE vegetation found that this flora is more closely related to that of AM than it is to that of the SCAF, suggesting past connections between AM and the AF through the Caatinga during several periods of the Tertiary and Quaternary (Santos et al., 2007). The existence of forested corridors connecting closely related populations of birds, amphibians, reptiles and small mammals with an extant disjunct distribution in AM and AF (Batalha-Filho et al., 2013a; Costa, 2003; Dal Vechio et al., 2019, 2018; Prates et al., 2016a; Thomé et al., 2016) is also supported by data from speleothems, palynological, paleoclimatic simulations and isotypes (Auler et al., 2004; Bouimetarhan et al., 2018; Cheng et al., 2013; Sobral-Souza et al., 2015) and could have had a significant influence in the processes of the PCE diversification. Teixeira & Gonzaga (1983a, 1983b) proposed that these connections did not affect all species in the same fashion, depending on their elevational range. Based on morphological comparisons, they suggested that the PCE avifauna is composed of two distinct groups with different evolutionary histories. The first group comprises species that occur in highland forests (>~550 m) and that, presumably, are close relatives of SCAF species. The second group is formed by species restricted to the lowlands and that are putatively related to Amazonian species. Teixeira & Gonzaga (1983a) suggested that this stratified distribution is a consequence of Quaternary climatic oscillations whereby dry climates would have restricted forest ranges and isolated populations to the highlands, and current lowland populations would have resulted from recent colonization events from Amazonia. Although these proposed mechanisms disagree with some recent studies (Carnaval and Moritz, 2008; Silveira et al., 2019), to date, these ideas remain untested with avian molecular data.

The advent of demographic modeling provides rigorous ways of directly testing the fit of empirical data to theoretical biogeographic models (Alvarez-Presas et al., 2014; Amaral et al., 2013; Carnaval et al., 2009; Oswald et al., 2017; Portik et al., 2017; Prates et al., 2016a; Thomé et al., 2016). Also, comparative phylogeographic analyses can be used to test for shared vicariant events affecting co-distributed species (Avise and Walker, 1998; Edwards and Beerli, 2000; Hickerson et al., 2007; Leaché et al., 2020; Xue and Hickerson, 2015). In this study, we combine demographic modeling and comparative phylogeographic analyses to test the PFR and RB hypotheses, as well as to assess the biogeographic affinities of birds occurring at different elevations (e.g., Amaral et al., 2018a; Oswald et al., 2017; Prates et al., 2016b; Thom et al., 2018; Thomé and Carstens, 2016). Specifically, we assembled and analyzed a dataset consisting of 5,060 ultraconserved elements (UCEs) and one mitochondrial gene for seven avian taxa endemic to the PCE and their closest relatives in order to i) reconstruct their phylogenetic history; ii) describe their population structure; iii) assess whether there is a relationship between the origin and the current elevation of populations; iv) test whether patterns of populational divergence and demographic history are concordant with either the PFR or the RB hypotheses; v) describe the demographic history of AF endemic populations (divergence time, migration pulses, population size changes), and vi) assess whether there is a shared biogeographic history across populations restricted to the PCE.

2. Material and methods

2.1. Taxon sampling

We selected seven forest taxa (*Phaethornis margarettae camargoi*, *Thalurania watertonii*, *Picumnus pernambucensis*, *Platyrinchus mystaceus niveigularis*, *Hemithraupis flavicollis melanoxantha*, *Tangara cyanocephala aff. corallina* and *Caryothraustes brasiliensis*) as a subset of the avifauna endemic to the PCE. Some of these taxa occur primarily in the lowlands (i.e., 0–550 m.a.s.l.; *Caryothraustes brasiliensis*, *Hemithraupis flavicollis*, and *Phaethornis margarettae camargoi*), whereas others occur both in the lowlands and highlands (i.e., 0–900 m.a.s.l; *Thalurania watertonii*, *Picumnus pernambucensis*, *Platyrinchus mystaceus niveigularis* and *Tangara cyanocephala aff. corallina*). Although *Tangara cyanocephala* and *Platyrinchus mystaceus* do not have a disjunct distribution pattern between AM and the AF, the inclusion of these taxa in our analyses aimed primarily at unraveling the evolutionary history of their populations in the AF.

We sampled the closest population to each taxon occurring in AM and the SCAF, and, in some cases, our sampling extended into the Andes and Central America. We defined the populations included in our analyses based on i) the existence of recognized subspecies (*Caryothraustes*, *Hemithraupis*, *Picumnus*, *Tangara, Platyrinchus*); ii) current geographic distribution patterns; iii) previously published phylogenies and taxonomic revisions (Barker et al., 2015; Benz et al., 2006; Burns et al., 2014; Klicka et al., 2007; McGuire et al., 2014; Piacentini, 2011; Rêgo et al., 2014; Tello and Bates, 2007; Tonetti et al., 2017), and iv) a preliminary assessment of mtDNA variation relative to potential closely-related taxa (unpublished data). For simplicity, hereafter, we will refer to these groups by their generic names, unless using specific or subspecific names is necessary. Species names follow the taxonomic classification of the Brazilian Ornithological Records Committee (CBRO; Piacentini et al., 2015), except for *Caryothraustes* for which we followed the proposal by Tonetti et al. (2017).

2.2. DNA extraction and sequencing of mitochondrial DNA

Total genomic DNA was extracted from pectoral muscle using PureLink® Genomic DNA Mini Kits (Invitrogen) following the manufacturer's protocol, including an RNAse treatment. We generated sequences for the mitochondrial gene NADH dehydrogenase 2 (ND2; 1,041 base pairs) for a total of 490 samples (*Caryothraustes* – 34, *Hemithraupis* – 17, *Phaethornis* – 54, *Picumnus* – 29, *Platyrinchus* – 107, *Tangara* – 31, and *Thalurania* – 158) and then, guided by these results, we selected 210 samples (*Caryothraustes* – 20, *Hemithraupis* – 15, *Phaethornis* – 24, *Picumnus* – 17, *Platyrinchus* – 64, *Tangara* – 15, and *Thalurania* – 55) for sequencing of ultraconserved elements (UCEs). All samples were from vouchered specimens housed in natural history collections (Supplementary Table S1). For *Tangara cyanocephala cearensis* we had no access to fresh tissue materials. Therefore, we extracted DNA from toepads of museum specimens using the established protocol by McCormack et al. (2016). We did these extractions in a facility separated from the one dedicated to DNA extractions from fresh tissue samples to avoid contamination. We quantified DNA concentrations using a Qubit fluorometer (Life Technologies, Inc.).

We amplified and sequenced the mitochondrial marker ND2 following protocols described elsewhere (Brumfield et al., 2007; Hackett, 1996; Sorenson et al., 1999). We edited DNA sequencing chromatograms using the software Geneious 9.1.2 (www.geneious.com, Kearse et al., 2012). Finally, we aligned sequences using ClustalW (Larkin et al., 2007) and confirmed that they did not include stop codons using Geneious. Newly obtained sequences were deposited in GenBank (Accession numbers: MT427781 – MT427831; MT437296 – MT437346; MT462982 – MT463138; MT471062 – MT471093; MT471103 – MT471261).

2.3. Mitochondrial DNA gene trees and haplotype networks

To visualize relationships between individuals across all sampled populations, we built median-joining networks using the software PopART 1.7 (Leigh and Bryant, 2015) after trimming regions of missing data in the ND2 alignments. Using complete alignments (1041 bp), we inferred mitochondrial gene trees within a maximum likelihood framework implemented in RAxML 7.2.7 (Stamatakis, 2006) on the Cipres Science Gateway v 3.1 (Miller et al., 2010). We conducted analyses using a GTR-GAMMA model with 100 independent searches, and estimated nodal support with 1000 bootstrap replicates. We inferred Bayesian time-calibrated gene trees using Beast 2.4.8 (Bouckaert et al., 2014). We used jModelTest 2.1.6 (Darriba et al., 2012) to select the best-fitting model of nucleotide substitution using the Akaike Information Criterion (AIC). We implemented a coalescent constant population size tree prior to all taxa, except for *Thalurania* that had a Yule process speciation tree prior. We used a relaxed uncorrelated lognormal clock and an ND2 mutation rate of 0.001 mutations/site/million years (Fleischer et al., 1998). We performed two independent runs for 100 million generations, sampling every 1000 generations. We verified whether runs reached desirable mixing and a stable posterior distribution by checking that the effective sample size values (ESS) were higher than 400 using Tracer 1.6 (Rambaut et al., 2015).

We used LogCombiner 2.4.5 and TreeAnnotator 2.4.5 to build a Maximum Clade Credibility Tree (MCCT, Bouckaert et al., 2014), with a burn-in of 10%. Visual plots of the trees with stratigraphic congruence were constructed using the *strap* R package (Bell and Lloyd, 2015). Finally, using DNAsp v6.1 (Rozas et al., 2017) we estimated population genetics summary statistics and performed neutrality tests for all haplogroups uncovered in the gene trees (Table S2).

2.4. Target capture of ultraconserved elements (UCEs)

We followed a sequence capture approach that targeted UCEs (Faircloth et al., 2012) to generate data from thousands of unlinked loci scattered throughout the genome. Although UCEs are essentially invariable across unrelated taxa, their flanking regions harbor genetic variability that is informative for phylogeographic and population genetic studies (Amaral et al., 2018a; Harvey et al., 2016; McCormack et al., 2013; Smith et al., 2014a; Thom et al., 2018; Zarza et al., 2018). We used standard library preparation protocols to enrich for 5,060 UCEs loci (Faircloth et al., 2012), targeting a set of 5,372 specific probes (MYbaits_Tetrapods-UCE-5 K kit; Mycroarray). The genomic enrichment and Illumina sequencing were performed by RAPiD Genomics (Gainesville, FL, USA) using at least 1,000 ng of input genomic DNA for each sample.

2.5. Sequence quality control, UCE assembly and SNP calling

After sequencing, we conducted quality control, assembly, and alignment using the Phyluce 1.6 pipeline (Faircloth, 2015). We first removed low-quality regions, adapters, and barcode contamination using Illumiprocessor 2.0.7 (Faircloth, 2013), a wrapper for Trimmomatic 0.32.1 (Bolger et al., 2014). We used Trinity 2.0.6 (Grabherr et al., 2013) to assemble contigs, and contigs were matched to the target probes using the function *match_contigs_to_probes.py*.

We extracted single nucleotide polymorphisms (SNPs) using an adapted version of a customized pipeline to perform SNP calling (Harvey et al., 2016) that is based primarily on Phyluce. Reads from each individual were mapped against reference-assembled contigs using the function *phyluce_snps_bwa_align.py*. We selected one reference individual per species complex based on coverage, number, and size of assembled contigs. This function uses the BWA_MEM algorithm (Li and Durbin, 2010) to index reference contigs and aligns raw trimmed reads against the reference. It then uses Picard (http://broadinstitute.github.io/picard/) to edit the output BAM file and mark PCR duplicates. This step generates one BAM file per individual that is subsequently merged into a single BAM file containing all individuals per species complex with Picard (MergeSamFiles.jar) and indexed with SAMtools (Li et al., 2009). We also created a reference sequence dictionary with Picard that was indexed with SAMtools.

The merged BAM and the reference sequence dictionary were used for final SNP calling using GATK (McKenna et al., 2010). We located indel intervals (RealignerTargetCreator), realigned (IndelRealigner), and called SNPs and indels (UnifiedGenotyper) with the merged BAM. We then ran a variant filtration (VariantFiltration) into the resulting calls to mask poorly validated SNPs. Filtered SNPs were submitted to the function "ReadBackedPhasing" to obtain phased alleles for each locus with a quality threshold of 20.0. We selected one random SNP per locus to avoid the bias of linkage disequilibrium. Finally, we removed Z-linked loci to prevent bias related to sex-chromosomes based on a Blastn (Altschul et al., 1997) search against the zebra finch Z chromosome (Ensemble taeGut3.2.4).

2.6. Analyses of population structure using SNPs

To infer the number of ancestral populations (*K*) and to assign individuals to their corresponding genetic cluster, we performed coefficients of mixture analyses with sparse nonnegative matrix factorization for clustering (sNMF; Frichot et al., 2014), implemented in the package LEA (Frichot et al., 2015) in R 3.4.3 (R Development Core Team, 2016). We evaluated values of *K* ranging from 1 to 10 and performed 100 replicate runs per each *K* value. We selected the best value of *K* as the run that obtained the lowest cross-entropy value. When differences in cross-entropy values between different values of *K* were small (i.e., difference of 0.001), we also considered the second-best *K* for downstream analyses. We assessed the robustness of these results by running sNMF using four different values of the α regularization parameter (10, 50, 100, 500). To uncover hidden population structure in large samples, we re-ran sNMF using specific populations subsets only (e.g., just AF or AM populations).

We also conducted Discriminant Analyses of Principal Components

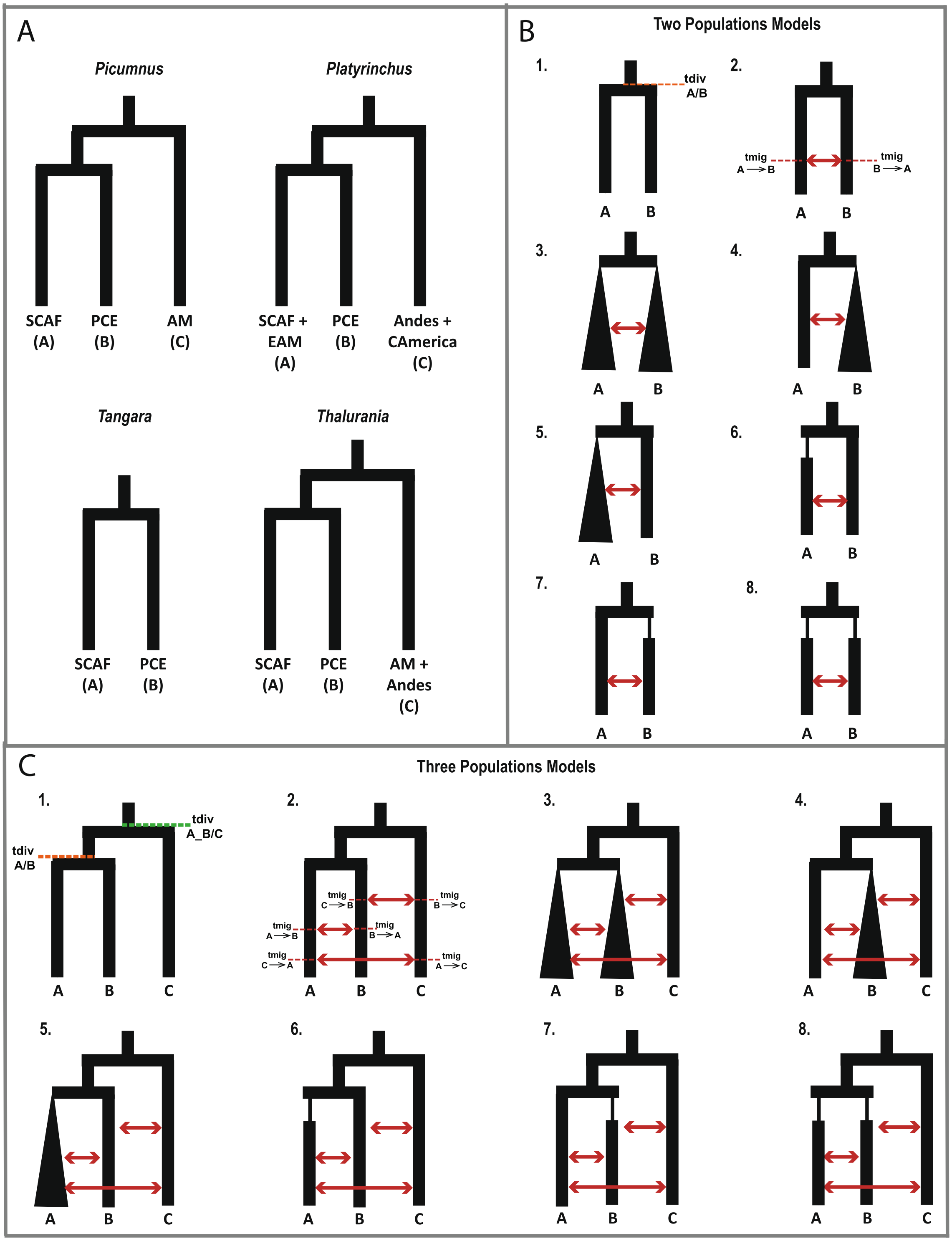

Fig. 2. Demographic models tested in *momi2* using UCE-derived SNP data. (A) Population structure and tree topology adopted for each study group. (B) Schematic of the alternative demographic models tested in *momi2* for groups with two populations (i.e., *Tangara*). Numbers represent the 8 tested models. (C) Schematic of the alternative demographic models tested in *momi2* for groups with three populations (i.e., *Picumnus, Platyrinchus*, *Thalurania*). Numbers represent the 8 tested models. Model parameters are noted as follows: *tdiv A/B*: divergence time between population A and B; *tdiv A_B/C*: divergence time between ancestral population A_B and population C; *tmig A-> B*: migration time from population A to B; *tmig B-> A*: migration time from population B to A; *tmig A-> C*: migration time from population A to C; *tmig C->A*: migration time from population C to A; *tmig B-> C*: migration time from population B to C; *tmig C->B*: migration time from population C to B. Acronyms: SCAF – Southern-central Atlantic Forest; PCE – Pernambuco Center of Endemism; AM – Amazonia; CAmerica – Central America, EAM – Eastern Amazonia.

(DAPC) in the *adegenet* R package (Jombart et al., 2010). We ran the k-means function (*find.clusters*) to infer the *a priori* number of genetic clusters in our samples based on the Bayesian Information Criterion (BIC). We included in the analyses the first set of principal components accounting for 80% of the variance.

2.7. Species tree analyses

We used the SNP dataset to infer a coalescent-based species tree using SNAPP (Bryant et al., 2012) implemented in BEAST 2 2.4.8 (Bouckaert et al., 2014). We defined species following the results of the population structure analyses and removed individuals with more than 40% of admixture coefficient to avoid violations of the assumption of independent lineages of the coalescent model. Using the defaults priors, we performed two independent runs of SNAPP for 3 million generations sampling every 1,000 steps and a burn-in of 10%. We verified whether runs reached desirable mixing and a stable posterior distribution by checking that the effective sample size values (ESS) were higher than 400 using Tracer 1.6 (Rambaut et al., 2015). We used LogCombiner and TreeAnnotator to build maximum clade credibility trees (MCC) with a burn-in of 10% (Bouckaert et al., 2014). We used DensiTree v2.2.6 (Bouckaert and Heled, 2014) to visualize the complete set of likely species trees.

2.8. Demographic modeling

To assess contrasting hypotheses about the diversification processes within the AF, we tested alternative demographic scenarios within a model-based framework. We used only those species complexes in which the PCE population formed a distinct genetic cluster in at least one of the methods of population structure analyses (i.e., *Thalurania*, *Picumnus*, *Platyrinchus*, *Tangara*; see details below). We defined populations following the results of population structure analyses. Hence, we considered two populations for *Tangara* (PCE and SCAF), and three for *Picumnus* (AM, SCAF, and PCE), *Platyrinchus* (PCE, SCAF, and Andes + Central America) and *Thalurania* (PCE, SCAF, and AM + Andes). Because most of the clustering analyses distinguished two populations in the AF for *Picumnus* (i.e., mtDNA and DAPC), except for sNMF when including all individuals, we performed demographic modeling using three populations. For *Thalurania*, our population scheme mirrors currently recognized species limits (*T. watertonii*, *T. glaucopis*, and *T. furcata*), albeit with *T. colombica* included in *T. furcata* (See details below).

For taxa with two or three populations, we organized demographic models according to the hypotheses they represent (Fig. 2B & C): 1) RB – A model with no population size changes without gene flow (model 1) and extremely low gene flow after divergence, representing a vicariant process (model 2); 2) PFR – Models that account for population expansion in the PCE or/and SCAF; the presence of bottlenecks in the PCE or/and SCAF, representing long term isolation in putative refugial areas, and the existence of gene flow after divergence (models 3–8). Because our primary interest was assessing demographic processes within the AF, we did not model changes in population size in AM, Andes, and Central America. The rationale behind including these populations in our models was to infer whether they affected genetic diversity in the AF via migration events or secondary contact.

Before testing alternative demographical scenarios, we used whole sequences for all loci to estimate the following demographic parameters in the software G-PhoCS 1.3 (Gronau et al., 2011): i) Effective population size (Ne) of current and ancestral populations scaled by $\theta = 4Ne\mu$, where μ is mutations per nucleotide site per generation; ii) divergence time between populations calculated from the parameter τ ($\tau = T\mu/g$, where T is the absolute divergence time in years, g is the average generation time), and iii) gene flow between populations as the number of migrants per generation. We generated alignments containing between 2,008 and 4,189 UCEs depending on the taxa and ran G-PhoCS for all the taxa following the population assignments of the structure analyses (Table S3; Fig. S15). We performed two sets of G-PhoCS analyses using different priors of τ and θ parameters (α-β: [prior 1: 1, 5000], [prior 2: 1, 50]), and gamma distribution ($\alpha = 0.002$ and $\beta = 0.001$) for the migration prior. We ran the multi-threaded version for 1,000,000 iterations with a 10% burn-in, with sampling for parameters done every five iterations. We assessed convergence and mixing by checking the effective sample size (ESS) value of each estimated parameter in Tracer 1.6 (Rambaut et al., 2015). We used a mutation rate of 2.5×10^{-9} substitution per site per generation (Nadachowska-Brzyska et al., 2015) to scale the parameter estimates.

We built empirical demographic models and compared them with simulated models using the program *momi2* (Kamm et al., 2019). *Momi2* (Moran Models for Inference) is a Python package that computes the expected site-frequency spectrum (SFS) and uses it to fit demographic histories within a coalescent framework. The main advantages of *momi2* compared to similar software usually employed in this type of analysis (e.g., fastsimcoal2, Excoffier et al., 2013) are i) the ability not only to construct a demographic history for a set of populations but also to plot the model and check whether it corresponds to expectations; ii) the possibility of scaling more populations than it was previously possible while considering complex demographic histories, including admixture; iii) faster computational times, and iv) its user-friendly platform (Kamm et al., 2019). First, we imported the SNP dataset into the *momi2* environment to compress and index the *vcf* file. A BED file obtained from the *vcf* file was used along with the population assignment to produce an allele count file. We then used the allele count file to generate the SFS with the function *momi.extract_sfs*. We incorporated the observed SFS into an inference procedure to assess the most informative model given the observed data. We constructed the different demographic models represented in Fig. 2 to test putative demographic scenarios within the AF. We used the function *momi.DemographicModel*, including those parameters to be considered (population size, divergence time, and migration rate) and tested the model fit with the function *model.optimize*, which yields a log-likelihood value. We used the value of the current effective population size (Ne) estimated with G-PhoCS (Table S3) for each population considered per taxa and a fixed value of 1e-5 for the growth rate parameter based on previous runs and Kamm et al. (2019) to reduce the complexity of the models and avoid model over-parametrization. Other parameters (e.g., divergence times, migration times, and migration rates) were estimated in *momi2* according to each historical model we tested. We used a mutation rate of 2.5x10^-9 substitution per site per generation (Nadachowska-Brzyska et al., 2015), the same employed in G-PhoCS to scale parameter estimates. For all taxa, we used a generation time of 2.3 years, which was previously used for a suboscine passerine bird (genus *Pyriglena*) with a socially non-promiscuous mating system (Maldonado-Coelho, 2012). To avoid potential biases arising from the use of a suboscine generation time across all of our taxa, we also built models using taxon-specific generation times obtained from the IUCN (IUCN, 2019; see Supporting Information, Table S3 and S4, and Fig. S14). We performed 100 replicate runs per model and selected the run with the highest log-likelihood to be used in the model selection procedure using the Akaike Information Criterion (AIC, Akaike, 1973). Also, we ran 100 bootstrap replicates of the best-fitting model to obtain a confidence interval for parameter values by randomly resampling the observed SFS and reestimating the parameters under the most likely model.

2.9. Testing for synchronous population divergences in the Atlantic Forest

We used the program *ecoevolity* v0.3.2 (Oaks, 2019) to test whether the events of divergence between the PCE and SCAF occurred synchronously or independently across the four species groups for which we modeled their demographic history. *Ecoevolity* is a full-likelihood Bayesian approach that directly calculates the likelihood of the population history from genomic data by analytically integrating over gene trees and sampling the model average posterior via Markov chain Monte

Carlo algorithms (Oaks, 2019; Oaks et al., 2019a, 2019b). Oaks (2019) found that this method can be more accurate at estimating the number and timing of divergence events across pairs of populations while requiring several orders of magnitude less computational time, than other existing approximate-likelihood approaches (Hickerson et al., 2006; Huang et al., 2011; Oaks, 2014). We conducted the analysis using the biallelic matrixes containing only those populations pairs in the AF. We used a value for the concentration parameter of the Dirichlet process that corresponds to the mean number of four events of divergence ($\alpha = 2.5$). To scale effective population sizes and divergence times by the mutation rate, we set the mutation rate parameter to 1. Thus, we obtained time in the expected number of substitutions per site. We assumed a prior on divergences times of $\tau \sim$ Gamma (2, 0.005). To assess the sensitivity of the results to these priors, we also analyzed the data under two additional priors on the concentration parameter (half of the prior probability on four events) and event times ($\tau \sim$ Gamma (0.2, 0.005)). We ran 3 MCMC chains for 50,000 generations, sampling every 50 generations for each prior setting. We assessed convergence and mixing of the chains using the *pyco-sumchains* tool, which reports the log-likelihood score, potential reduction factor (PSRF), and the effective sample size (ESS) of for all continuous parameters. We also inspected the chains visually in Tracer 1.6 (Rambaut et al., 2015). As the MCMC chains converged almost immediately, we conservatively removed the first 101 samples from each chain.

3. Results

3.1. Mitochondrial haplotype networks and gene trees

Haplotype networks showed that all populations that are endemic to the PCE shared no haplotypes with populations in AM or the SCAF (Fig. S1). However, some PCE haplotypes were more similar to those from the SCAF, as observed for *Caryothraustes,* than they were to other haplotypes in the PCE (Fig. S1). Except for *Thalurania* and *Platyrinchus*, PCE haplotypes were more similar to haplotypes from the SCAF, which in many cases were separated by only one or two mutational steps (e. g., *Caryothraustes*, *Hemithraupis*, *Phaethornis*), than they were to those from AM. Also, for all taxa, but *Caryothraustes*, gene trees inferred using both maximum likelihood and Bayesian inference (Supplementary Figs. S2–S8) recovered a monophyletic PCE phylogroup. Gene trees for *Hemithraupis*, *Phaethornis*, *Picumnus*, and *Tangara* showed distinct phylogroups representing the SCAF and PCE populations. However, only in *Phaethornis* and *Picumnus* the SCAF populations were unambiguously sister to those in the PCE.

Time-calibrated gene trees supported a Pleistocene divergence of the PCE population from the SCAF (Supplementary Figs. S2–S8) in almost all groups. However, there was incongruence across taxa regarding divergence times. *Phaethornis* and *Caryothraustes* showed the most recent (~0.38 Ma) divergences, whereas *Tangara* the oldest one (~2.4 Ma). *Hemithraupis* (~1.2 Ma) and *Picumnus* (~1.0 Ma) showed intermediate divergence times during the Mid-Pleistocene. For *Thalurania,* the gene tree topology revealed that the PCE population belonged within the Amazonian group (*T. furcata*) and dated its divergence to the late Pliocene (2.8 Ma). Finally, the PCE population of *Platyrinchus* was recovered as sister to a clade comprising all other populations of this species complex and diverged from them at the end of Pliocene (2.6 Ma). In all cases, the associated confidence intervals also included divergence dates into the early Pleistocene.

3.2. UCE-based analyses of population structure

After adapter and contamination removal, we obtained an average of 3,326,939 read pairs per sample. We were able to assemble an average of 9,369.24 total contigs per sample with a mean coverage of 21.15X. We obtained a total of 21,627–71,493 bi-allelic SNPs per taxon, with a maximum of 63 SNPs per locus. The final SNP datasets used in subsequent analyses had one SNP randomly sampled per UCE locus and contained between 1,833 and 4,014 SNPs per species complex (see Table 1 for details).

We uncovered three patterns of population structure across taxa (Fig. 3). The first pattern supported only one ancestral population in AM and one in the AF, thus clustering the PCE endemic taxa with individuals from the SCAF. We observed this pattern in *Caryothraustes, Hemithraupis,* and *Picumnus* using both clustering methods (Fig. 3). The second structuring pattern identified two populations in the AF, those north (PCE) and south of the São Francisco River (SCAF). We found this pattern in *Platyrinchus*, *Tangara*, and *Thalurania* (Fig. 3). In the third pattern, observed only in *Phaethornis*, we found no structure between AF individuals from those in AM (Fig. 3). For 4 of the seven study groups (*Hemithraupis*, *Picumnus*, *Thalurania*, *Phaethornis*), both clustering methods yielded conflicting results (Fig. 3; S11 and S12). However, regardless of the number of identified clusters, the signal of AM populations being distinct from those in the AF held, and changes reflected internal rearrangements within those groups (see Supplementary Materials). In *Hemithraupis,* besides the inference of one population in the AF and one population in AM ($K = 2$), we found high probability for the existence of two populations in AM due to similar values of BIC and cross-entropy in the DAPC analysis and the second most informative model in sNMF ($K = 3$) (Fig. 3, S9-S12, Tables 2). In *Picumnus*, we observed that the second-best sNMF model and the DAPC analysis identified two populations within the AF ($K = 3$), providing evidence for the PCE as a distinct population (Figs. S9-S12; Table 2). DAPC analysis also detected two clusters in Amazonia (Figs. S11 and S12). Also, an additional sNMF run that included individuals only from the AF supported two differentiated populations in AF (PCE and SCAF, K = 2, Fig. 3). *Thalurania* also exhibited disagreements regarding the best number of ancestral populations in the two structuring analyses. Although sNMF supported five populations (alpha parameter = 50; cross-entropy = 0.1995; Table 2), DAPC supported four (Figs. S11 and S12). In this case, the discordance came from whether we were able to separate individuals from extreme western AM from the remaining western AM individuals. We detected admixed individuals in the Guiana Shield, Southern Bahia, and the Purús-Juruá interfluvium (Fig. 3). In *Tangara* and *Platyrinchus,* we did not find discordances in the number of ancestral populations when we compared the two clustering algorithms (Fig. 3, S11 and S12). However, the separation of the Andean population from Central America and the Chocó was the key feature in separating the two most informative clustering scenarios in *Platyrinchus* (Fig. S10). In *Phaethornis,* sNMF analyses yielded support for four populations ($K = 4$, alpha parameter = 50; cross-entropy = 0.49): i) Northern Amazonia (*P. s. superciliosus*), ii) West of Madeira River (*P. s. ochraceiventris*), iii) Madeira-Tapajós interfluvium (*P. s. insignis*) and iv) eastern Amazonia (*P. s. muelleri*), AF (*P. m. margarettae* and *P. m. camargoi*), and a range of admixed individuals from the Xingú and Tocantins interfluvium (Fig. 3). However, the DAPC analysis provided support for the AF as a genetically distinct population ($K = 5$; Figs. S11 and S12). Admixed populations were detected in southern AM for *Caryothraustes*, in northern AM for *Hemithraupis*, and in eastern AM for *Picumnus* (Fig. 3).

3.3. Species trees

Except for *Phaethornis* and *Thalurania*, we resolved species trees with high support (posterior probability [PP] > 0.98, Fig. 3). In these two cases, species tree conflicts arose primarily between Amazonian populations. In those cases for which we identified PCE populations to be genetically distinct (*Platyrinchus*, *Tangara*, *Thalurania*), we found evidence for them to be sisters to populations in the SCAF (SCAF + eastern AM, in the case of *Platyrinchus*), albeit with no statistical support in *Thalurania* (PP = 0.74). In turn, we found these AF clades to be sisters to AM populations. In those cases that population structure analyses uncovered only one genetically distinct population in the AF, we found no conflict in recovering AF populations as sister to AM populations. For all

Table 1

Summary of the UCE sequencing results for each study group. N: Number of individuals; Mean total bp: mean total number of base pairs per sample; N total SNPs: Total number of SNPs per group; N Loci (1 SNP per locus): Number of loci included in the final SNP dataset, considering that we extracted one SNP per target locus; Mean depth: Average sequence coverage across target loci.

Species group	N	Mean read pairs	Mean total bp	Mean number contigs	Mean coverage (X)	N total SNPs	Mean SNPs per locus (min–max)	N Loci (1 SNP per locus)	Mean depth	Mean % of missing data
Caryothraustes	20	3,009,065.71	325,082,627	10,948.72	19.21	86,284	22.55 (1–63)	3,826	22.21	7.45%
Hemithraupis	15	2,947,493.86	304,835,675	10,948.72	19.21	61,951	16 (1–46)	3,871	21.97	6.18%
Phaethornis	24	2,776,964.04	302,591,320.4	10,212	20.75	49,119	11.81 (1–40)	3,996	22.38	3.27%
Picumnus	17	3,058,690.76	300,322,194.8	7,287.70	23.4	25,803	6.62 (1–28)	3,839	19.29	4.77%
Platyrinchus	64	4,368,376.57	448,161,671.7	10,214.32	19.77	45,077	24.52 (1–67)	1,833	32.69	7.69%
Tangara	15	2,704,328	276,646,208.9	8,411.53	21.17	38,370	9.54 (1–34)	3,950	22.94	10.04%
Thalurania	55	3,022,935.2	321,703,638.8	8,752.26	22.6	71,493	17.81 (1–45)	4,014	28.41	2.99%

groups, species tree topologies were generally similar to those inferred using mtDNA, except for *Thalurania*. In the mtDNA analyses, the PCE population (*T. watertonii*) fell within AM populations.

3.4. Demographic modeling of populations endemic to the Pernambuco Center of Endemism

The demographic history of all four taxa with independent PCE populations (*Thalurania*, *Platyrinchus*, *Picumnus*, and *Tangara*) was consistent with a model of isolation with migration and constant population size (model 2, Table 3, Fig. 2). The magnitude and direction of migration events varied across taxa, but in general, demographic modeling was consistent with migration events in and out of the PCE (Table 4). For instance, in *Tangara* and *Picumnus* we found evidence of high levels of migration (~20% of N_e) between the PCE and SCAF at different times (Table 4). Nevertheless, in *Picumnus,* the confidence interval pointed to a high probability of lower migration levels between the two AF populations. Similarly, we detected signals of gene flow between the AF populations in *Platyrinchus* and *Thalurania,* but they were higher from the PCE to the SCAF (11.1% and 15.5% of N_e, respectively) than they were from the SCAF to the PCE (0.6% and 3.49% of N_e, respectively). We also detected migration events between the AF (PCE or SCAF) and AM. *Picumnus* exhibited the lowest values, most of them close to zero, and they corresponded to migration from the PCE to AM and from the SCAF to AM. Migration values from the SCAF to AM were significant, despite being very low (1.3% and 1.15% of N_e, respectively). *Thalurania* exhibited high values of migration between the AF and AM in all possible directions (see Table 4), with the lowest values from the SCAF to AM (8.2% of Ne). In *Platyrinchus*, although values were close to zero, migration events between the SCAF (and eastern AM) and the populations in the Andes and Central America were detected at lower rates than migration events between the SCAF and PCE populations (Table 4).

Using *momi2*, mean divergence times between the PCE and the SCAF corresponded to the Mid-Pleistocene and ranged from 0.24 to 0.74 Ma with confidence intervals (CI) from the parametric bootstrapping extending from 0.16 to 0.79 Ma (Table 4). *Picumnus* showed the most recent divergence time (0.24 Ma, CI: 0.204–0.298 Ma), whereas *Thalurania* had the oldest mean divergence (0.74 Ma, CI: 0.163–0.79 Ma), although the confidence interval suggested that this divergence could be more recent than the inference for *Picumnus*. *Platyrinchus* and *Tangara* had intermediate and overlapping values of divergence times within the AF (0.65, 0.63 Ma, respectively; Table 4). Mean divergence times between the AF and AM ranged from 0.39 to 1.37 Ma (CI 0.19–1.40 Ma) in *Thalurania* and *Picumnus*. We found the youngest divergence for *Picumnus*, whereas *Thalurania* had the oldest one, albeit with a wide CI (Table 4). The AF (PCE and SCAF) + eastern AM population of *Platyrinchus* diverged from its sister population from the Andes and Central America 0.76 Ma (CI: 0.64–0.78 Ma). Migration times varied across taxa suggesting they were not synchronous and ranged from Middle to Upper Pleistocene (Table 4).

The estimation of divergence times using G-PhoCS was broadly concordant with those obtained with *momi2* (Table 4 and Tables S3). For instance, for *Picumnus*, *Tangara,* and *Thalurania,* although G-PhoCS estimated more recent divergence times between the PCE and SCAF than *momi2*, they were, on average, only 0.1 Ma younger. Similarly, the divergence time between AM and the AF for *Picumnus* was slightly older than the value estimated by *momi2* (0.52 Ma against 0.40 Ma), but for *Thalurania,* G-PhoCS inferred a more recent divergence (0.74 Ma against 1.37 Ma). Both values of divergence times estimated for *Platyrinchus* are virtually the same when compared to *momi2*, showing only minimal variation (see Table 4, and Table S3). G-PhoCS estimates of current effective population sizes were generally higher in the SCAF and AM or Andes (+ Central America) than they were in the PCE, probably due to the PCE's current distribution being restricted (see Table S3). *Picumnus* was the taxon that had the lowest values of population size in the AF (PCE – 31,153; SCAF – 25,159), whereas *Platyrinchus* showed the highest values, specifically for the SCAF (PCE – 127,963; SCAF – 487,866), probably due to its wide distribution that extends to eastern AM.

3.5. Testing for shared events of divergence in the Atlantic Forest

Results from the test of shared evolutionary history using *ecoevolity* supported a model of no shared divergence events across taxa in the AF (Fig. 5). This result was consistent across scenarios considering alternative priors of the concentration parameter on the Dirichlet process and divergence times. This pattern of asynchronous divergences seemed to be partially incongruent with results from our demographic modeling, but a correct understanding of the assumptions of the models can explain these differences. Results from *momi2* suggested the possibility that *Platyrinchus* and *Tangara* had similar estimates of divergence time, but *ecoevolity* supported a younger divergence time for *Platyrinchus*. Also, the putative chronological order in which AF populations split according to *ecoevolity* differed from those recovered by *momi2* and G-PhoCS. This apparent disagreement between analyses can be reconciled based on the fact that *ecoevolity* does not account for gene flow (Oaks, 2019; Oaks et al., 2019). Thus, as *momi2* estimated significant gene flow for most of the taxa, the time inferred by *ecoevolity* could reflect the last time the populations experienced significant gene flow, raising the apparent disagreement between analyses (Oaks et al., 2019b). Nonetheless, the fundamental result of asynchronous divergence across taxa was consistent based both on demographic analyses and by *ecoevolity*.

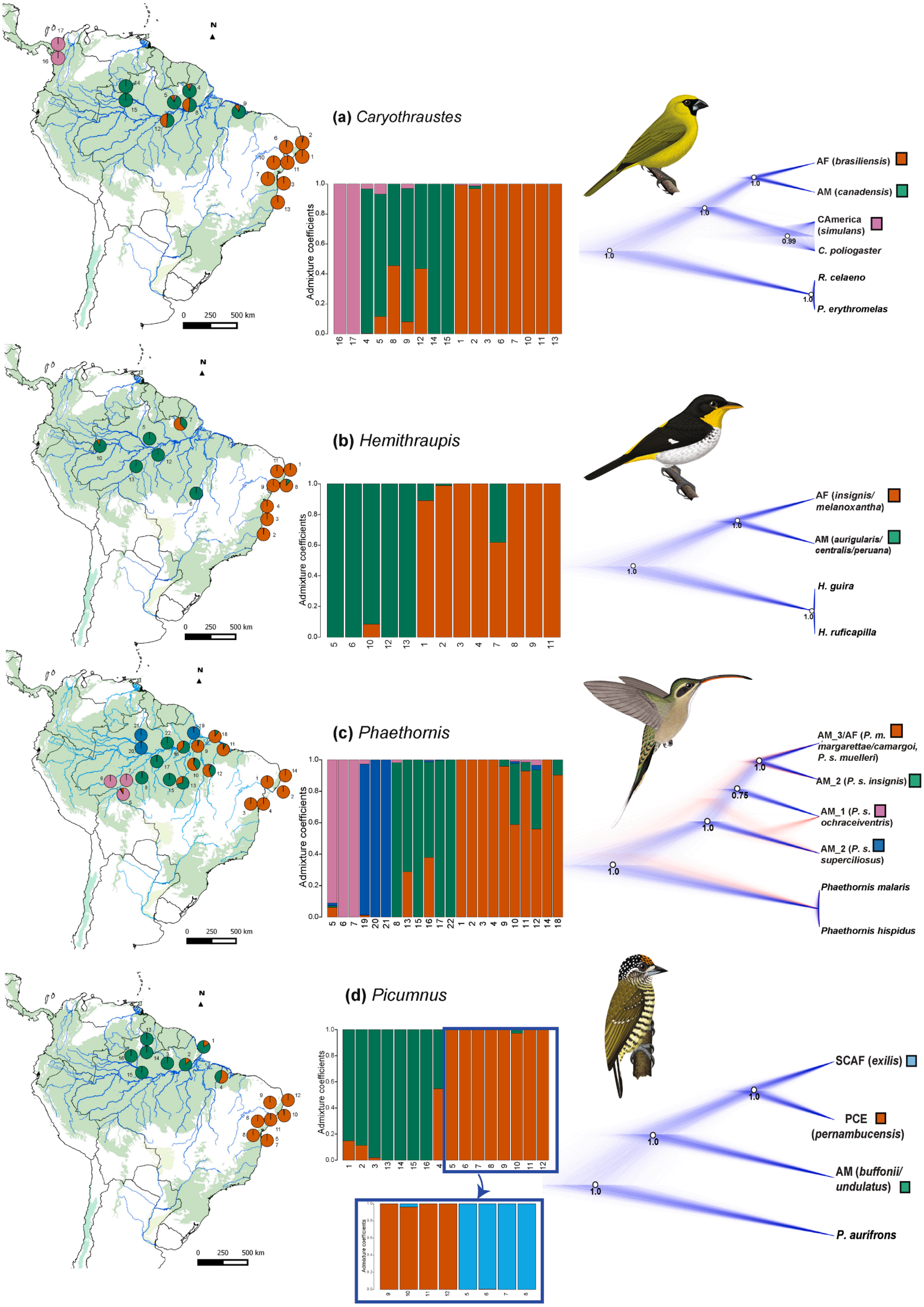

Fig. 3. Population structure and species tree analyses of seven species complexes occurring in the PCE. (a) *Caryothraustes* (3,826 SNPs); (b) *Hemithraupis* (3,871 SNPs); (c) *Phaethornis* (3,996 SNPs); (d) *Picumnus* (3,839 SNPs); (e) *Platyrinchus* (1,833 SNPs); (f) *Tangara* (3,950 SNPs); (g) *Thalurania* (4,014 SNPs). Left: Maps with pie charts representing admixture coefficients (K with lowest cross-entropy values) for each sample as quantified by sNMF. Center: Bar plots showing admixture coefficients per sample for the best value of K. In *Picumnus* the inset represents the substructure analysis performed with AF samples only. Right: Claudograms of species tree inferences. Numbers at nodes represent posterior probability values of the 50% Maximum Clade Credibility Tree. Colored squares represent populations as colored on maps. Acronyms: SCAF – southern-central Atlantic Forest; PCE – Pernambuco Center of Endemism; AM – Amazonia, CAmerica – Central America, NAM – Northern Amazonia, WAM – Western Amazonia, EAM – Eastern Amazonia. Species illustrations made and provided with permission by F. Ayerbe-Quiñones.

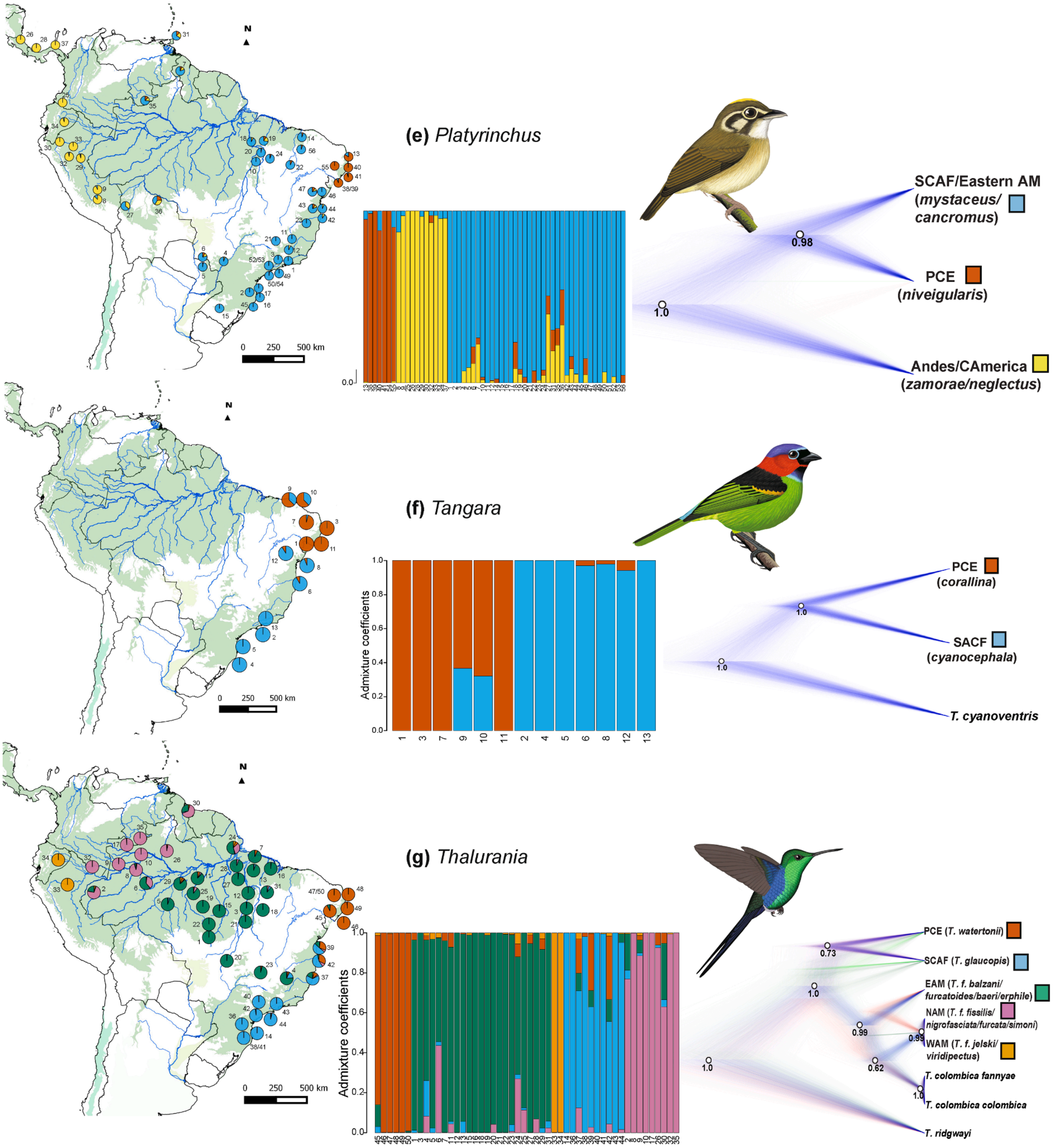

Fig. 3. (*continued*).

4. Discussion

Here, we presented the first comparative phylogeographic study that included phylogenetic, population structure, and demographic analyses based on a combination of mitochondrial and UCE-derived sub-genomic data to shed light on the evolutionary history of avian populations restricted to the PCE. We showed that PCE populations were more closely related to populations in the SCAF than they were to populations in AM (Fig. 3, S1-S12). Also, we showed that population structuring levels were generally low within the AF, with some PCE-restricted taxa (*Caryothraustes*, *Picumnus*, *Hemithraupis*, and *Phaethornis*) being genetically indistinguishable from populations in the SCAF (Fig. 3). Furthermore, we recovered a demographic history for those PCE endemics that was consistent with a pattern of divergence with gene flow, with no signal of rapid population expansions or contractions (model 2, Figs. 2 and 4). Divergence times between the PCE and the SCAF were dated to the Mid-Pleistocene, supporting the idea of the Pleistocene Pernambuco refugium and rejecting the role of the São Francisco River as a primary barrier for gene flow that promoted population differentiation in the AF. At best, our results suggested that this river has been a permeable secondary barrier for some of the populations that it dissects (Table 4).

4.1. *Population structure and phylogeographic relationships in the Pernambuco Center of Endemism*

Our results favored a common pattern of sister relationships between populations in the PCE and the SCAF, with varying levels of genetic divergence, and did not support close relationships between the PCE and AM. This pattern of populations in the PCE being sisters to populations in the SCAF has been described for some AF taxa (e.g., Schultzde et al.,

Table 2

Summary of the two most informative clustering schemes under different values of the α regularization parameter as identified by sNMF. Lower cross-entropy values denote better models.

	α = 10	α = 50	α = 100	α = 500
Caryothraustes				
best K value	**K = 3**	K = 3	K = 3	K = 3
(cross-entropy)	**(0.5985)**	(0.6024)	(0.6129)	(0.6088)
second-best K value	K = 2	K = 2	K = 2	K = 2
(cross-entropy)	(0.6169)	(0.6169)	(0.6188)	(0.6226)
Hemithraupis				
best K value	K = 2	**K = 2**	K = 2	K = 2
(cross-entropy)	(0.8058)	**(0.8037)**	(0.8056)	(0.8136)
second-best K value	K = 3	K = 3	K = 3	K = 3
(cross-entropy)	(0.8304)	(0.8192)	(0.8184)	(0.8428)
Phaethornis				
best K value	K = 3	**K = 4**	K = 4	K = 4
(cross-entropy)	(0.4975)	**(0.4949)**	(0.5141)	(0.5029)
second-best K value	K = 4	K = 5	K = 3	K = 3
(cross-entropy)	(0.499)	(0.5024)	(0.5149)	(0.5083)
Picumnus				
best K value	K = 2	K = 2	**K = 2**	K = 2
(cross-entropy)	(0.6754)	(0.6729)	**(0.6544)**	(0.6652)
second-best K value	K = 3	K = 3	K = 3	K = 3
(cross-entropy)	(0.6823)	(0.6937)	(0.6684)	(0.6913)
Platyrinchus				
best K value	K = 5	K = 3	**K = 3**	K = 3
(cross-entropy)	(0.2281)	(0.2313)	**(0.2267)**	(0.2287)
second-best K value	K = 4	K = 4	K = 4	K = 4
(cross-entropy)	(0.2315)	(0.2351)	(0.2296)	(0.2297)
Tangara				
best K value	K = 2	K = 2	**K = 2**	K = 2
(cross-entropy)	(0.8819)	(0.8703)	**(0.8700)**	(0.9006)
second-best K value	K = 3	K = 3	K = 3	K = 3
(cross-entropy)	(0.9406)	(0.8974)	(0.9314)	(0.9557)
Thalurania				
best K value	K = 5	**K = 5**	K = 5	K = 5
(cross-entropy)	(0.2011)	**(0.1995)**	(0.2011)	(0.2024)
second-best K value	K = 4	K = 4	K = 3	K = 4
(cross-entropy)	(0.203)	(0.2019)	(0.2032)	(0.2024)

Table 3

Summary of the results of demographic model selection with *momi2*. Values of composite likelihood (Max ln(likelihood)); number of parameters of the model (N Parameters); Akaike Information Criterion (AIC); the difference between AIC values of each model and that of the best-ranked model (ΔAIC); and Akaike weights (ω_i) for the first three best-ranked models of each taxon. Model numbers refer to the schematic models defined in Fig. 2.

Model	Max ln (likelihood)	N parameters	AIC	Δ AIC	ω_i
Picumnus					
2	−12586.346	14	25200.693	0	1
5	−12613.074	14	25254.148	53.455	2.467E−12
6	−12621.289	14	25270.579	69.886	6.673E−16
Platyrinchus					
2	−4230.624	14	8489.248	0	1
4	−4249.77	14	8527.541	38.293	4.838E−09
7	−4251.686	14	8531.373	42.124	7.124E−10
Tangara					
2	−8764.022	5	17538.045	0	1
1	−8819.465	1	17640.930	102.884	4.559E−23
7	−8972.906	5	17955.812	417.766	1.918E−91
Thalurania					
2	−7086.421	14	14200.842	0	1
4	−7130.471	14	14288.942	88.100	7.400E−20
7	−7153.548	14	14335.096	134.254	7.032E−30

Table 4

Demographic parameters estimate inferred with *momi2* for the best-ranked models of each taxon and 95% confidence intervals. tdiv: Divergence time; tmig: Migration time; mig rate: Percentage of N_e that migrated; ***: parameter not considered in the model. Populations letter as defined in Fig. 2.

Taxon	*Picumnus*	*Platyrinchus*	*Tangara*	*Thalurania*
tdiv A/B	0.23 Ma (0.20–0.29 Ma)	0.64 Ma (0.63–0.65 Ma)	0.62 Ma (0.55–0.76 Ma)	0.74 Ma (0.16–0.79 Ma)
tdiv A_B/C	0.39 Ma (0.35–0.52 Ma)	0.75 Ma (0.63–0.78 Ma)	****	1.37 Ma (0.18–1.39 Ma)
tmig A → B	0.058 Ma (0.057–0.059 Ma)	5E-3 Ma (5 e-E-3–5.01E-3 Ma)	0.176 Ma (0.11–0.22 Ma)	0.26 Ma (0.16–0.29 Ma)
tmig B → A	0.058 Ma (0.057–0.059 Ma)	5.19E-3 Ma (4.25E-3–5.2E-3 Ma)	0.10 Ma (0.07–0.12 Ma)	0.11 Ma (0.005–0.12 Ma)
tmig C → B	0.034 Ma (0.034–0.034 Ma)	0.14 (0.12–0.15 Ma)	****	0.18 Ma (0.04–0.18 Ma)
tmig B → C	0.07 Ma (0.07–0.08 Ma)	0.37 (0.34–0.37 Ma)	****	0.22 Ma (0.005–0.23 Ma)
tmig C → A	0.21 Ma (0.21–0.22 Ma)	0.033 Ma (0.03–0.035 Ma)	****	0.72 Ma (0.16–0.73 Ma)
tmig A → C	5.07E-3 Ma (5E-3–5.11E-3 Ma)	0.07 Ma (0.07–0.08 Ma)	****	0.11 Ma (0.10–0.12 Ma)
mig rate A → B	20% (0.01–20%)	0.60% (0.15–6.3%)	19% (13.2–20%)	3.49% (4E-6–3.53%)
mig rate B → A	20% (0.01–20%)	11.10% (9.1–22%)	20% (19.8–20%)	15.50% (6.3–15.7%)
mig rate C → B	0.00% (3.8E-5–4E-5%)	20% (20–40%)	****	20% (19.5–20%)
mig rate B → C	1.30% (0.8–2.0%)	20% (0.09–20%)	****	19.50% (6.48–20%)
mig rate C → A	0.00% (2.8E-5–3E-5%)	5.30% (4.4–22.5%)	****	20% (6E-6–20%)
mig rate A → C	1.15% (0.46–1.41%)	2.60% (1.9–24.7%)	****	8.20% (2E-6–8.25%)

2016; Weir and Price, 2011), often supported by breaks in phenotypic data (e.g., Zimmer, 2008; Rêgo et al., 2014). Nevertheless, other studies that included PCE endemic taxa have recovered a close relationship with Amazonian taxa that conflict with our results (Batalha-Filho et al., 2014; Maldonado-Coelho et al., 2013; Tello et al., 2014; Thom and Aleixo, 2015). In some of those cases that exhibited a PCE–AM sister relationships, taxa such as *Cercomacra laeta sabinoi* and *Thamnophilus aethiops distans* (Thom and Aleixo, 2015) belonged to primarily Amazonian species complexes with no representatives in the SCAF. In the case of *Pyriglena pernambucensis* and *Conopophaga cearae*, each has a congener in the SCAF which occupies a very similar ecological niche.

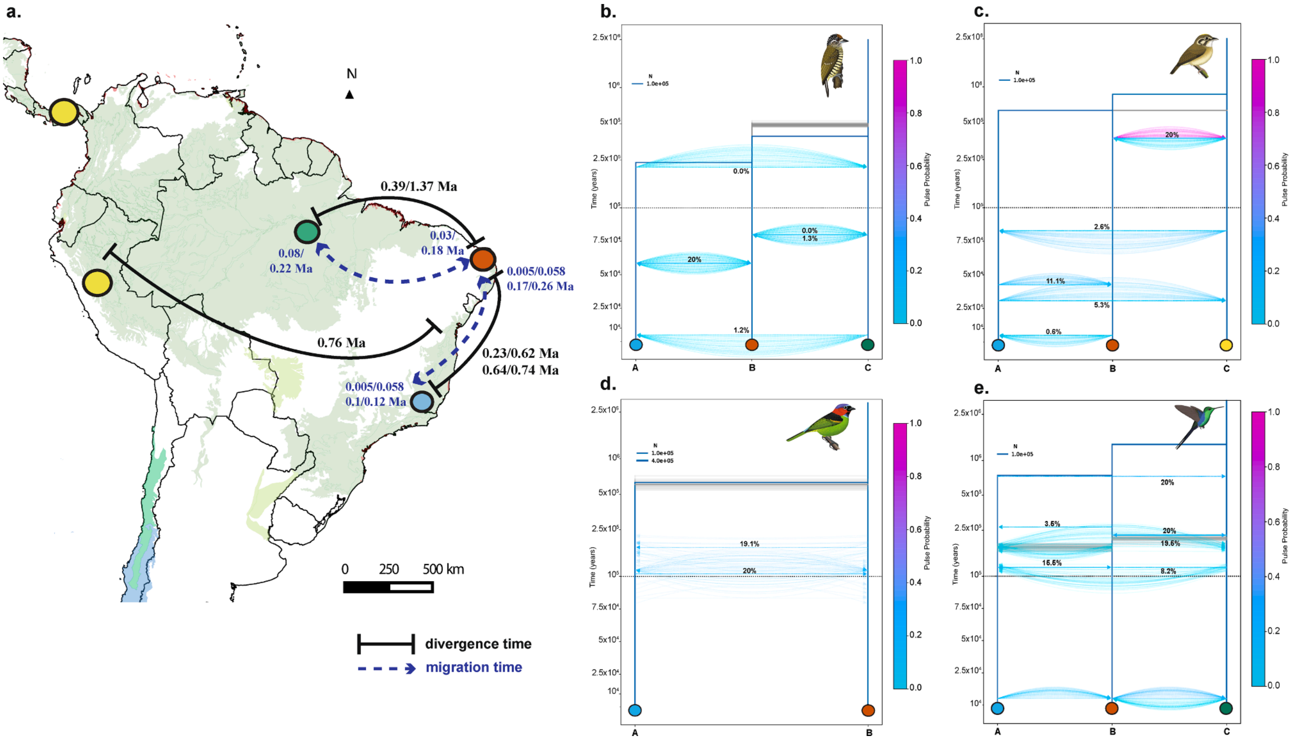

Fig. 4. (a) Summary map showing the putative divergence and migration times between the main areas of this study as inferred by *momi2*. Divergence times are represented by solid black lines. Migration times are represented by dashed blue arrows. Values represent the chronological order estimated across the four species complexes. (b) Schematic of the demographic model and parameter estimates for *Picumnus* with the bootstrap replicates (model 2 in Figs. 2, 3,839 SNPs); (c) Schematic of the demographic model and parameter estimates for *Platyrinchus* with the bootstrap replicates (model 2 in Fig. 2; 1,833 SNPs); (d) Schematic of the demographic model and parameter estimates for *Tangara* with the bootstrap replicates (model 2 in Fig. 2; 3,950 SNPs); (e) Schematic of the demographic model and parameter estimates for *Thalurania* with the bootstrap replicates (model 2 in Fig. 2; 4,014 SNPs). Values associated with migration events (light blue arrows) represent the percentage of Ne that migrated. Letters represent the populations as defined in Fig. 2. Species illustrations made and provided with permission by F. Ayerbe-Quiñones. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

We observed an intriguing pattern of no population structure within the AF in *Caryothraustes*, *Hemithraupis, Picumnus*, and *Phaethornis*. This pattern was not anticipated because those taxa have well-defined diagnostic phenotypic characters in the PCE (Piacentini, 2011; Tonetti et al., 2017). Also, because phylogeographic structure in the AF has been detected even in taxa without evidence of phenotypic differences (Amaral et al., 2013; Batalha-filho et al., 2019; Batalha-Filho et al., 2014; Batalha-Filho and Miyaki, 2016; Menezes et al., 2016; Silveira et al., 2019), it was unexpected to find a contrasting pattern of no phylogeographic structure in the face of phenotypic differentiation. A lack of population structure across the AF is known for some avian taxa endemic to the PCE (Batalha-Filho et al., 2012; Cabanne et al., 2013), albeit none of these studies considered populations with apparent morphological differences. Amaral et al. (2018) suggested that in datasets comprising few loci, such as in *Antilophia* manakins, uncoupling between phenotype and genotype could be the result of low statistical power to identify shallow divergences. Amaral et al. (2018) also argued that the use of sub-genomic makers (UCEs) might enable the detection of genetic structure that other more tradicional loci (mitochondrial and intron data) do not show (Luna et al., 2017). On the other hand, mtDNA revealed shallow divergences between PCE and AF populations (except for *Caryothraustes*), presumably due to its faster substitution rates and smaller effective population size. Nonetheless, understanding the underlying causes of this incongruence is not trivial because these two classes of markers reflect different genomic processes (Brito and Edwards, 2009). It has been noted that working with a single matrilineal locus, such as mtDNA, can yield inadequate representations of genomic coalescent histories that are more susceptible to the effects of stochastic processes and that are often insufficient to detect the signals of gene flow and introgression (Bravo et al., 2019; Degnan and Rosenberg, 2009; Edwards, 2009; Edwards and Bensch, 2009; Hudson and Turelli, 2003; Moore, 1995). In light of this, it appears that analyses of UCEs represent a more appropriate method to summarize genomic variation and to estimate parameters of demographic histories (Harvey et al., 2016).

The lack of structure in these four species appears to reflect scenarios of divergence with gene flow in the face of large scale historical processes (Amaral et al., 2018). We detected gene flow in taxa with structured populations (e.g., *Tangara* and *Platyrinchus*), suggesting that it could be a common feature of PCE populations. In the case of unstructured populations, gene flow occurring at different times in the past could have erased genetic variation preventing it from being captured by the markers we used, resulting in a pattern of panmixia. Alternatively, they could also represent a single panmictic population with current gene flow among individuals, and morphological differences could have arisen quickly through a localized divergent selection process (Edwards et al., 2016; Edwards and Bensch, 2009; Zamudio et al., 2016). Robust approaches such as whole-genome resequencing could allow the identification of putative genes under natural selection responsible for the observed phenotypic variation (Campagna et al., 2017; Lamichhaney et al., 2015).

4.2. *The demographic history of populations restricted to the Pernambuco Center of Endemism: The role of Pleistocene forest refugia and rivers*

The PFR invokes allopatric divergence with initial isolation during glacial periods followed by expansion and secondary contact during interglacial phases. In contrast, the RB hypothesis considers gene flow at the river headwaters only and predicts no dramatic demographic fluctuations (Carnaval and Moritz, 2008; Haffer, 1969; Maldonado-Coelho et al., 2013; Thomé et al., 2014). Given the expectations of the PFR

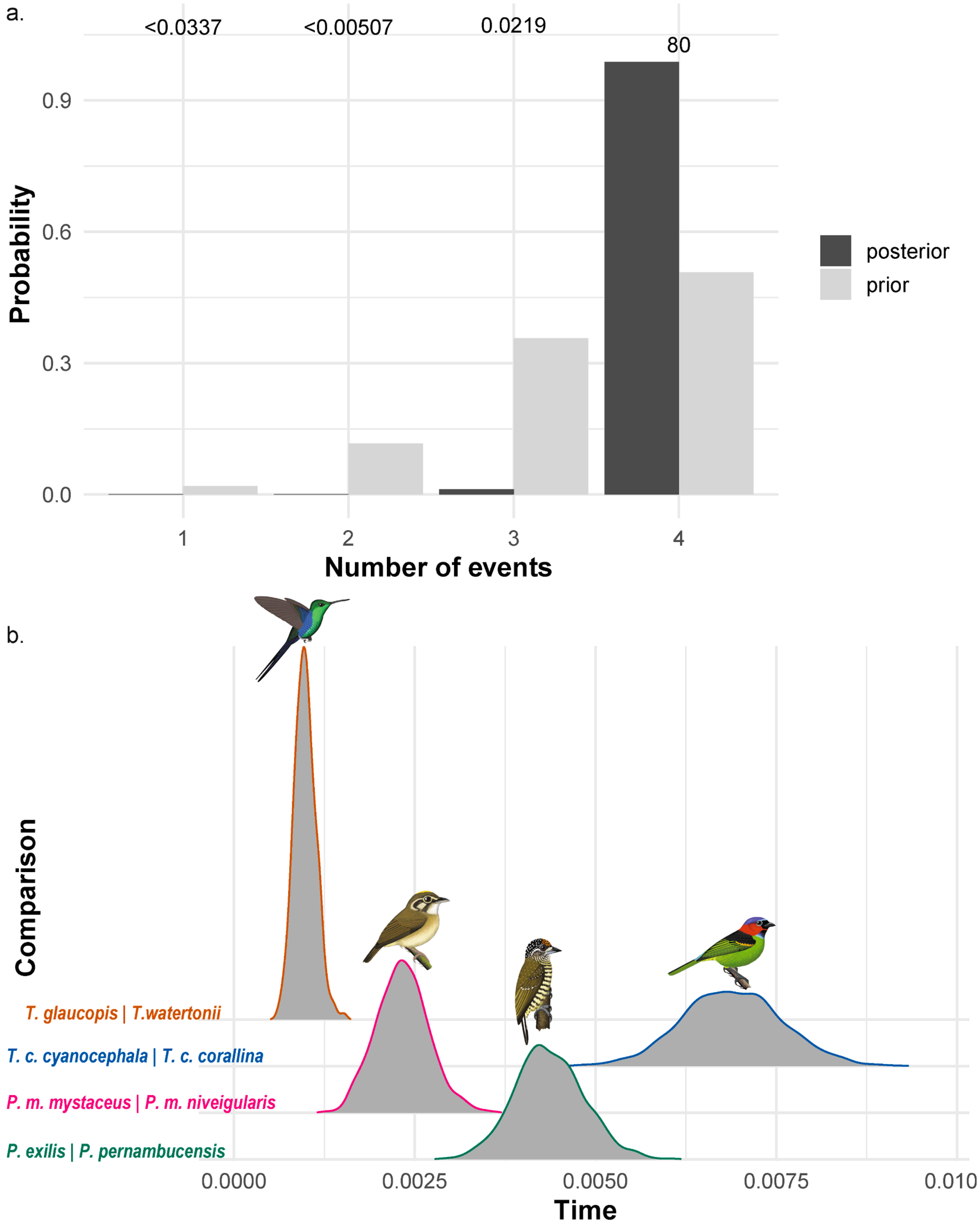

Fig. 5. Results of the test of simultaneous divergences across taxa in *Ecoevolity*. (a) Approximate prior (light bars) and posterior (dark bars) probabilities of the number of divergence events across the four populations pairs in the SCAF and PCE (*Picumnus*, *Platyrinchus*, *Tangara*, and *Thalurania*). (b) Approximate marginal posterior densities of divergence times (in expected substitutions per site; left present, right past) for each pair in the SCAF and PCE. Species illustrations made and provided with permission by F. Ayerbe-Quiñones.

and the stability-extinction model, PCE populations should have had increased demographic stability, especially during the LGM, and populations south of the Doce River should have exhibited more substantial demographic fluctuations and signals of recent colonization from the north.

For all of our species groups (*Picumnus*, *Platyrinchus*, *Tangara*, and *Thalurania*), demographic modeling results were consistent with an allopatric model of divergence with gene flow with no rapid changes in population sizes. Considering that for all species the most informative model was that of no changes in population size (model 2), one could infer strong support for the RB hypothesis. However, a more nuanced assessment of specific details of these models, such as recent divergence time and high levels of gene flow between the PCE and the SCAF, provides substantial support for the occurrence of Pleistocene forest refugia and argues against the RB hypothesis. For instance, *Picumnus exilis* and *P. pernambucensis* are restricted to putative regions occupied by the Bahia and Pernambuco refugia of the LGM (*sensu* Carnaval et al., 2009). Therefore, our result of no recent changes in population size in these taxa is in agreement with the stability-extinction model (Carnaval and Moritz, 2008).

The São Francisco River is one the largest rivers in the AF, and although previous research has suggested that it might have a role in driving population differentiation (Cabanne et al., 2008; Roda et al., 2011; Rodrigues, 1996; Silva et al., 2004), no evidence supports this statement (e.g., Bolívar-Leguizamón et al., 2020; Maldonado-Coelho et al., 2013). This river is ancient, and the origin of its paleodrainage was dated to the Miocene (Lundberg et al., 1998; Potter, 1997), making it much older than the estimated Mid-Pleistocene origin of our target PCE endemics and previous studies (e.g., Cabanne et al., 2008). Thus, it seems implausible that this river acted as a universal primary barrier for gene flow. Furthermore, the evidence of several waves of migration events between all the populations in the PCE and SCAF implies that the São Francisco River is a highly permeable barrier for secondary contact, similar to other AF rivers such as the Jequitinhonha River (Batalha-filho et al., 2019).

Recent studies suggest that the Pleistocene climatic history of the Atlantic Forest was more dynamic than advocated by hypotheses such as the PFR and the stability-extinction model (Amaral et al., 2016; Cabanne et al., 2016; Leite et al., 2016b). We propose that a highly dynamic history of recurrent Pleistocene climatic oscillations in South America (Cheng et al., 2013; Cruz et al., 2009; Nace et al., 2014; Wang et al., 2017; reviewed by Baker et al., 2020) split ancestral populations spanning the entire AF, favoring the occurrence of forest refugia, such as the PCE. Nonetheless, this idea of refugia is somewhat divorced from the notion of synchronous refugia distributed across the continent that were equally affected by continental climate (sensu Haffer, 1969). Instead, these refugia might represent the outcome of a dynamic sequence of wet-and-dry cycles that generated persistent forest expansions and contractions, thereby creating opportunities for divergence and admixture events (Bolívar-Leguizamón et al., 2020; Prates et al., 2016). This scenario is in line with the idea that ranges of populations in humid forests could have been larger during glacial maxima than they were during interglacial ranges (Cabanne et al., 2016; Leite et al., 2016a; Mascarenhas et al., 2019; Silveira et al., 2019) because of possible expansions into areas currently covered by dry environments, such as the Cerrado and Caatinga, or even into the continental shelf due to the retraction of the sea level (Cabanne et al., 2016; Leite et al., 2016a; Silveira et al., 2019). This notion is also supported by palynological and vegetation data (Arruda et al., 2018; Bouimetarhan et al., 2018; Costa et al., 2018; Dupont et al., 2010; Ledru et al., 2016; Silveira et al., 2019) as well as by phylogeographic and demographic histories of other AF birds (Amaral et al., 2013, 2018a; Amaro et al., 2012; Pie et al., 2018).

The close relationship between the PCE and the SCAF is, therefore, a consequence of a once continuous population spanning the entire AF that was split as a consequence of climatic cycles with subsequent expansions during interglacial periods. Given that we recovered signals of migration events between these two areas in some of our target taxa, these populations are likely not reproductively isolated, and ongoing gene flow favors their homogenization, preventing structured geographic clustering.

4.3. The association between elevation and patterns of geographic structure

Our analyses included three taxa that occur primarily at lower elevations (*Caryothraustes*, *Hemithraupis,* and *Phaethornis*) and four that occur both in the lowlands and highlands (*Thalurania*, *Picumnus*, *Platyrinchus,* and *Tangara*; Mariano, 2014). The diversification scenario based on species elevational ranges (Teixeira and Gonzaga 1983a, 1983b) and subsequent studies of the PCE avifauna (Batalha-Filho et al., 2013b; Maldonado-Coelho et al., 2013; Tello et al., 2014; Thom and Aleixo, 2015) predicted that lowland taxa in the PCE would be more closely related to Amazonian populations, and that highland taxa would be more closely related to SCAF populations. However, except for *Thalurania*, our analyses strongly supported a close connection between the PCE and the AF populations located south of the São Francisco River, regardless of the elevational range of populations. According to Teixeira et al. (1986), Quaternary climatic oscillations probably shaped the distribution of highland species because dry climates during the LGM would restrict forest ranges and isolate them in the highlands. A recent study found that montane bird populations in the SCAF highlands were likely isolated in mountain tops during warm-interglacial periods (Amaral et al., 2018a) in a similar fashion to that described by Teixeira et al. (1986). Indeed, we could extend such an explanation to some taxa restricted to the highlands such as *Philydor novaesi*, *Cichlocolaptes mazarbarnetti*, *Terenura sicki*, and *Myrmotherula snowi*. However, we must consider that the PCE avifauna differs from that of the SCAF because they occupy a different climatic niche of warm-adapted organisms (Carnaval et al., 2014; Ledo and Colli, 2017) and that the PCE presumably did not present forest retraction during the LGM (Carnaval et al., 2009; Carnaval and Moritz, 2008; Silveira et al., 2019). Therefore, mountain tops were presumably not isolated from the lowlands as occurred in the regions south of Doce River, at least during the LGM.

Our molecular dating results suggested that the divergences of PCE populations were older than the LGM. *Platyrinchus* and *Tangara* currently occur in the highest elevation regions of the PCE and showed a partially synchronous divergence event (~0.6 Ma). Thus, we suggest that the isolation of these populations might be associated with one of the early – Mid-Pleistocene – wet-and-dry cycles that maintained them isolated in the highlands of the PCE, as previously shown for *Thamnophilus caerulescens cearensis* (Bolívar-Leguizamón et al., 2020) and previously proposed for high elevation species (Teixeira et al., 1986). Further analyses using highland-restricted species will be critical to test this pattern and the main predictions of Teixeira and Gonzaga (1983a, 1983b).

Taxa that occur predominantly in the lowlands not only showed a close relationship with the SCAF, but our analyses revealed that they are remarkably similar genetically. As stated above, an Amazonian origin of the lowland populations of the PCE is unlikely due to the climatic stability predicted in the Pernambuco refugium during LGM (Carnaval et al., 2009; Carnaval and Moritz, 2008; Silveira et al., 2019). However, we must state that Amazonia has indeed played a critical role in generating the extant composition of the PCE avifauna. Although populations from the PCE are closely related to SCAF populations, we should not ignore the role of connections with Amazonia in the formation of its genetic diversity. Our results from historical demography (*momi2* and G-PhoCS) showed that the AF populations diverged from AM during different periods of the Pleistocene (Table 4 and S3) and that, even after the divergence, intense migratory flows occurred connecting these regions. These results support the hypothesis that past forest expansions promoted the formation of forested corridors throughout the present-day dry diagonal, which enabled the connection between these two major forested areas in South America (Cheng et al., 2013; Dal Vechio et al., 2018; Prates et al., 2016a; Thomé et al., 2016). The area spanning the PCE was, in fact, distinct climatically from the SCAF and more similar to eastern AM (Carnaval et al., 2014; Cheng et al., 2013; reviewed by Baker et al., 2020). A precipitation dipole running from west to east in South American equatorial latitudes that cycled at orbital time scales (~20 ka) might have created reversed climatic regimes between western AM and eastern South America (Cruz et al., 2009; Wang et al., 2017). This dipole presumably brought the PCE and eastern AM under a similar climatic regime wherein forest corridors could have emerged connecting and disconnecting their biotas as climatic cycles occurred.

4.4. No evidence for a shared evolutionary history across populations restricted to the PCE

Although we found signals of extensive migration between populations, there was no support for synchronous events of divergence and migration across taxa, especially when considering that synchronous events inferred with *ecoevolity* might represent migration after divergence (Oaks et al., 2019b). On the contrary, our results argued for highly idiosyncratic histories of migrations waves that can be partially explained by numerous climatic cycles and species' ecological attributes that allow populations to separate and come into contact repeatedly (Burney and Brumfield, 2009; Smith et al., 2014b). We inferred migration events between the PCE and the SCAF to be idiosyncratic and ubiquitous in the taxa we studied (Figs. 4 and 5), and migration rates were more pronounced from the PCE to SCAF, suggesting that the PCE could have been a more stable forested region during Mid-Pleistocene that functioned as a source of individuals.

On the other hand, divergence times inferred via demographic modeling using *momi2* between the PCE and the SCAF suggested the possibility of one synchronous event during the Mid-Pleistocene involving two taxa. Although estimated divergence times varied across species (from 0.16 to 0.79 Ma), *Platyrinchus* and *Tangara* share comparable divergence times (Table 4), suggesting that they were subject to similar evolutionary pressures, such as shifts of forest distribution during glacial maxima (Hewitt, 2000, 2004). Our results showed that main divergence events between the PCE and neighboring forested regions took place during the Mid-Pleistocene (~0.2, 0.6 and 0.75 Ma) or even later during the late Calabrian Period if considering alternative generation times (0.4–1.32 Ma, Table S4). These estimates predate the LGM (upper Pleistocene ~ 0.02 Ka) and coincide with observations for a wide array of taxa (Bartoleti et al., 2018; Leite et al., 2016; Peres et al., 2015; Ribeiro et al., 2011; Thomé et al., 2014; Álvarez-Presas et al., 2011), including passerine birds with structured AF populations (Batalha-filho et al., 2019; Batalha-Filho and Miyaki, 2016; Cabanne et al., 2008; Dhorta et al., 2011; Mascarenhas et al., 2019). All the divergence times between the PCE and SCAF were estimated to have occurred after more pronounced longer glacial cycles had been initiated (Lambeck et al., 2002). Possibly, such cycles allowed the PCE to have acted as a stable environmental area, promoting isolation and vicariance during a prolonged period.

The likely synchronous divergence found in *Tangara* and *Platyrinchus* could be associated with their ability to colonize and persist in small forest fragments. Ecological traits, such as habitat preference and colonizing ability, are good predictors of population structure (Burney and Brumfield, 2009; Smith et al., 2014b), and discrepancies in species ecological attributes could ultimately affect their responses to climatic and paleogeographical changes (Batalha-Filho et al., 2012; Cabanne et al., 2016; Lavinia et al., 2019; Oswald et al., 2017; Smith et al., 2014a, 2012; Ströher et al., 2019; Thom et al., 2020). Even though all of our study taxa are tightly associated with forests, they all have tolerance for varying levels of forest fragmentation and degradation, and they seem to be common where they occur. Nonetheless, our experimental design and our selection of taxa limit our ability to quantitatively test the role of ecological traits in explaining population structure in the PCE. Future studies would benefit from directly including and testing ecological attributes of species (e.g., Thom et al., 2020).

5. Conclusions

We used a combination of population genetic analyses and demographic modeling of seven avian taxa endemic to the northernmost portion of the AF, known as the PCE, to shed light on the evolutionary history of its distinctive avifauna. To our knowledge, this is one of the most comprehensive comparative phylogeographic study on the birds of the northern Atlantic Forest in terms of the number of taxa and loci. Our results from mtDNA and genome-wide SNPs showed that PCE populations are more closely related to populations in the SCAF than they are to populations in AM without any association with species' elevational ranges. We detected low levels of genetic structure within the AF, and we found that some phenotypically divergent taxa restricted to the PCE are not genetically distinct from their relatives south of the São Francisco River (*Caryothraustes brasiliensis*, *Hemithraupis flavicollis melanoxantha*, and *Phaethornis margarettae camargoi*). The demographic history for those groups that presented two genetic clusters in the AF (PCE and SCAF) is consistent with an allopatric model of divergence in the Mid-Pleistocene with subsequent gene flow, and no signals of rapid changes in population size.

We found evidence for Pleistocene forest refugia to be essential players in shaping current diversity patterns in the AF, despite the lack of signal of population expansion and contraction. The recent divergence inferred during the Mid-Pleistocene and the evidence of the high posterior rate of gene flow led us to discard the role of the São Francisco River in the diversification of PCE restricted taxa. The allopatric divergence between PCE and SCAF populations could be related to once wide-ranged populations that became fragmented as a consequence of a climate-driven forest contraction (Haffer, 1969; Pennington et al., 2004; Smith et al., 2012). We found support for the stability-extinction model for *Picumnus*, which presented population stability in two areas of putative refugia (*sensu* Carnaval et al., 2009). The remaining taxa (*Platyrinchus*, *Thalurania*, and *Tangara*) did not show structured populations in the Bahia refugium or evidence of population expansion south of Doce River, contrasting with the predictions of the stability extinction model. Population stability in the SCAF demonstrated that the effects of the Pleistocene climatic oscillations could be different than previously assumed (Behling, 2002; Carnaval and Moritz, 2008). Our results support the idea that population ranges in the SCAF may have remained constant or even expanded during glacial maxima (Cabanne et al., 2016; Leite et al., 2016a; Silveira et al., 2019). Inferred divergence times showed that the diversification processes of the PCE-restricted taxa occurred in the Mid-Pleistocene in at least three different periods with a possible shared divergence time between *Tangara* and *Platyrinchus*. Migration pulses reconnecting populations in the PCE and SCAF were inferred as asynchronous events and ranged from middle to upper Pleistocene. Connections with Amazonia also played a significant role in the origin, and subsequent assembly of populations in the PCE probably contributed to its marked structure and divergence.

We suggest that the process of the community assembly of the PCE avifauna has been affected by the dynamic climatic history of South America, and its forest stability may have persisted through a prolonged time at least since Mid-Pleistocene. Persistent climatic fluctuations provided ample opportunities for population divergence and admixture through time, affecting different populations in mainly idiosyncratic manners. Further comparative phylogeographic studies with the use of ecological niche modeling of other taxa endemic to PCE are necessary for strengthening our understanding of the processes that produce and maintain the biological diversity of the PCE.

CRediT authorship contribution statement

Fernanda Bocalini: Conceptualization, Formal analysis, Funding acquisition, Investigation, Methodology, Resources, Supervision, Writing - review & editing. **Sergio D. Bolívar-Leguizamón:** Methodology, Software, Funding acquisition, Formal analysis, Writing - review & editing. **Luís F. Silveira:** Conceptualization, Funding acquisition, Resources, Supervision, Writing - review & editing. **Gustavo A. Bravo:** Conceptualization, Funding acquisition, Resources, Formal analysis, Investigation, Supervision, Methodology, Visualization, Writing - review & editing.

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Data statement

UCE raw read data are available on NCBI SRR 12743128-12743314 (BioProject PRJNA663543). VCF files and UCE sequence alignments are available on https://github.com/febocalini/PCE.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ympev.2020.106973.

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