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Research Article

Biogeographic scenarios for the diversification of a widespread Neotropical species, *Glossophaga soricina* (Chiroptera: Phyllostomidae)

CAYO A. ROCHA DIAS[1,2], JOSÉ E. SANTOS JÚNIOR[3,4], FERNANDO A. PERINI[1,2] & FABRÍCIO R. SANTOS[2,3,4]

[1]Laboratório de Evolução de Mamíferos, Departamento de Zoologia, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais, Av. Antônio Carlos 6627, 31270-010 Belo Horizonte, MG, Brazil
[2]Pós-Graduação em Zoologia, Universidade Federal de Minas Gerais, 31270-010 Belo Horizonte, MG, Brazil
[3]Pós-Graduação em Genética, Universidade Federal de Minas Gerais, 31270-010 Belo Horizonte, MG, Brazil
[4]Laboratório de Biodiversidade e Evolução Molecular, Departamento de Biologia Geral, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais, Av. Antônio Carlos 6627, 31270-010 Belo Horizonte, MG, Brazil

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In order to contribute to the understanding of the effect of geological and climatic changes on species diversification in the Neotropics, we employed molecular techniques to study the population dynamics of the glossophagine bat *Glossophaga soricina*, a widespread species in the Neotropical region. We aimed to assess the dispersal and distribution of mtDNA lineages of *G. soricina* and evaluate the possible effect of vicariant events in the population history and dynamics. *Glossophaga soricina* presented two main highly supported mtDNA lineages, which diverged between ~2.4 and 5 million years ago, probably following a vicariant event caused by the Andes final uplift. The lower sea level during Pleistocene glaciations also made possible the occupation of Jamaica after an event of dispersion over the Caribbean Sea, although past climatic fluctuations had little effect over population dynamics of *G. soricina*. Our results corroborate the idea that the Andes uplift played an important role in the evolution of Neotropical biodiversity. In this context we suggest that geographic events causing large scale environmental disjunction, such as the uplift of mountains, are more likely to restrict gene flow amongst populations of tolerant species with broad geographic range than local climate driven environmental changes.

Keywords: Bayesian Skyline, biogeography, Glossophaginae, neotropical, phylogeny, phylogeography, S-DEC, S-DIVA

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Introduction

Tropical regions harbour the greatest diversity of life on Earth. This fact reflects on the existence of a latitudinal gradient which is one of the oldest and best known diversity patterns (Hawkins, 2001). After decades of studies on tropical diversity, a plethora of hypotheses trying to explain this latitudinal gradient have emerged, although some of those have shown logical or evidential flaws (Pianka, 1966; Rahbek & Graves, 2001; Rhode, 1992; Willig, Kaufman, & Stevens, 2003).

Conceptually, biogeographic hypotheses can be formulated according to ecological and historical (evolutionary) explanatory elements. Traditionally, ecological hypotheses have been more extensively tested, although some have been considered inappropriate in explaining the observed patterns (Mittelbach et al., 2007). The ever-increasing availability of molecular techniques allows more direct tests of evolutionary and historical hypotheses once applied to intraspecific phylogenies (Diniz-Filho et al., 2008). In this context, Pavan, Martins, Santos, Ditchfield, and Redondo (2011) point out that vertebrate phylogeography, a discipline primarily concerned with the geographic distributions of genealogical lineages and its underlying processes (Avise et al., 1987), is an important tool for better understanding Neotropical biogeography and the models that try to explain its diversity.

Glossophaga soricina (Pallas, 1766) is a small nectar-feeding bat with a widespread distribution in the Neotropical region. It is known from Mexico to Argentina and occurs in many different habitats, ranging from arid-subtropical thorn forest to tropical rain forest and savannas (Alvarez, Willig, Jones, & Webster, 1991). In a comprehensive review, Webster (1983) reported the existence of

Correspondence to: Fabrício R. Santos. E-mail: fsantos@icb.ufmg.br

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five subspecies: *Glossophaga soricina antillarum*, *G. s. handleyi*, *G. s. mutica*, *G. s. soricina*, and *G. s. valens.* The same author pointed out that *G. s. soricina* could be easily distinguished from the other subspecies based on morphological characters. These apparent morphological discrepancies were later corroborated by molecular studies (Clare, 2011; Ditchfield, 2000; Hoffman & Baker, 2001; Webster, 1983).

Some of the first Neotropical bat phylogeography studies compared the phylogeographic patterns of bats and small non-volant Neotropical mammals (Ditchfield, 2000; Ditchfield & Burns, 1998). The results revealed low intraspecific sequence divergence for most studied species, except for one: *Glossophaga soricina*, with about 9% sequence divergence. Hoffman and Baker (2001) conducted phylogeographic studies on *G. soricina* and resumed the ideas of Webster (1983) about *G. soricina* being, in fact, two species. Later, these authors also suggested that the uplift of the Andes and the Panamanian land bridge were important events driving the diversification of bats, including *G. soricina* (Hoffman & Baker, 2003).

The present study uses molecular markers Cytochrome b, Cytochrome c Oxidase I and DEAD-box Y RNA helicase, and a more extensive individual sampling, to test biogeographic and historical hypotheses concerning the Neotropical bat *G. soricina.* We tried to answer the following questions: (i) Has *G. soricina* reached the Antilles from Central America as hypothesized by Baker and Genoways (1978)? (ii) Is the split between the main lineages related to the Andes uplift as proposed by Hoffman and Baker? The objectives of this study also comprised: (i) to describe the genetic diversity of the main lineages of *G. soricina*, (ii) to estimate the divergence time amongst the main lineages of *G. soricina* and correlate these dates with geological and historical events in the Neotropical region; (iii) to infer the ancestral areas where diversification processes occurred; and (iv) to contribute to the understanding of the processes that drove diversification in the Neotropics.

Materials and methods

Sampling

We analysed sequences of *G. soricina* used by Dávalos and Jansa (2004), Hoffman and Baker (2001), Hoffman, Hoofer, and Baker (2008) and Clare (2011), available at GenBank. We also added 24 new sequences generated in the present study for each mitochondrial marker (S1, see online supplemental material, which is available from the article's Taylor & Francis Online page at: http://dx.doi.org/10.1080/14772000.2016.1271060) in order to expand the sampling of *G. soricina* in Brazilian territory, which was scantily sampled in previous studies, even though it comprises roughly half of the range of the species. These sequences consisted of 96 localities along its distribution range (S2, see supplemental material online). As in previous studies, no sample of *G. s. mutica* was available; therefore this subspecies was not included in the analyses.

Molecular analyses were based on variations of the mitochondrial Cytochrome b (Cyt b) and Cytochrome c Oxidase I (COI) genes and nuclear DEAD-box RNA helicase Y chromosome gene (DBY). Due to differential sampling of the sequences, the analyses were based on three different datasets: (i) 74 Cyt b sequences, (ii) 100 COI sequences, and (iii) 64 DBY sequences.

DNA extraction, amplification, and sequencing

Except for DBY, whose sequences were exclusively obtained from GenBank, DNA was extracted from liver and muscle by the phenol-chloroform method (Sambrook & Russel, 2001). Primers and protocols used for the polymerase chain reaction and sequencing of Cyt b and COI was conducted as described in Folmer, Black, Hoeh, Lutz, and Vrijenhoek (1994) and Redondo, Brina, Silva, Ditchfield, and Santos (2008).

Phylogenetic inferences

DNA sequences were aligned using MAFFT 7 (Katoh & Daron, 2013), and visually inspected in Aliview (Larsson, 2014). Cyt b and COI sequences were concatenated using FASconCAT (Kück & Meusemann, 2010).

Three different phylogenetic methods were employed: maximum parsimony (MP), implemented in TNT (Goloboff, Farris, & Nixon, 2008), Maximum likelihood (ML), in RAxML 8 (Stamatakis, 2014), and Bayesian inference (BI), implemented in MrBayes 3.2.5 (Ronquist & Huelsenbeck, 2003). Phylogenetic analyses were performed using a concatenated matrix of Cyt b and COI genes and totalling 108 terminals.

Tree inference with MP was performed using a heuristic search, with 100 replications of random (stepwise) addition of taxa followed by TBR branch swapping. Partitioned ML and BI analyses used the substitution models, as indicated by jModelTest 2 (Darriba, Taboada, Doallo, & Posada, 2012). The best fit model for both markers was GTR + G + I. Bootstrap values were used as a measure of branch support for MP and ML phylogenies. For the BI, we conducted two independent runs with four Markov chains, along 40 million generations. Summarizing tree and parameter statistics was accomplished after discarding 25% of the samples as burn-in. Convergence between independent runs was assessed by inspection of standard deviation of split frequencies and potential scale reduction factor (PSRF).

Additionally, we generated Cyt b and COI networks in PopART (http://popart.otago.ac.nz) using the median-joining algorithm (Bandelt, Forster, & Röhl, 1999).

Intraspecific analyses

Genetic diversity patterns were calculated in DNAsp 5 (Librado & Rozas, 2009) through haplotype (h) and nucleotide diversity (π) and genetic distance amongst groups. We also performed Analysis of Molecular Variance (AMOVA; Excoffier, Smouse, & Quattro, 1992) conducted in Arlequin 3.5 (Excoffier & Lischer, 2010) in order to assess the hypothesis of population structure and the existence of geographic barriers.

Divergence time analyses

Divergence time analyses were conducted on BEAST 2 (Bouckaert et al., 2014), and were based on the Cyt b dataset, since this marker presented a more comprehensive phylogenetic sampling.

An uncorrelated log-normal relaxed clock (UCLN) was used, selected through a Bayes Factors analysis (S1, see supplemental material online), and the tree was modelled under a Yule process. The substitution model GTR + G was used, excluding the invariant sites parameter suggested by jModelTest 2, in order to attain a better mixing and avoid over-parameterization, since the estimation of invariant sites may lead to extra uncertainty in the analysis (Drummond & Bouckaert, 2015). As the only *Glossophaga* fossils described so far were all from the Pleistocene-Holocene boundary, consequently not informative for divergence time analyses, we employed a partial phylostomid (rooted on phyllostomine) phylogeny that was time-calibrated with fossils of *Notonycteris* and *Palynephyllum* (Czaplewski, Takai, Naeher, Shigehara & Setoguchi, 2003).

The relationship between the Miocene fossil *Notonycterys* (with an age range from 11.8 to 16.3 Ma) and *Vampyrum* has been proposed in recent works (Czaplewski et al., 2003; Dávalos, Velazco, Warsi, Smits, & Simons, 2014), therefore this fossil was used to incorporate a calibration point in the divergence between *Vampyrum* and *Chrotopterus*. We applied a lognormal distribution with a mean of 1, standard deviation of 0.8 and an offset of 11.2 Ma, leading to a Highest Probability Density (HPD) 95% of 11.8–24.2 Ma for this calibration point. Given the uncertainty in phylogenetic position of *Palynephyllum* (with an age range from 15.5 to 16.3 Ma), which has been considered a Glossophaginae by Czaplewski et al. (2003), and a Lonchophyllinae by Dávalos et al. (2014), we ran two sets of divergence time analyses. In the first, *Palynephyllum* age has been used to calibrate the basal divergence in Glossophaginae (applying to this node a lognormal distribution with a mean of 1, standard deviation of 0.5 and an offset of 15.5 Ma, leading to a HPD 95% of 15.8–17.9 Ma). In the second, this fossil was used to calibrate the basal divergence in Lonchophyllinae (applying to this node a lognormal distribution with a mean of 1, standard deviation of 0.5 and an offset of 15.5 Ma, leading to a HPD 95% of 15.8–17.9 Ma). The plausibility of both models has been assessed by Bayes Factors.

A calibration point was also incorporated in the root of the tree, applying a normal distribution with a mean of 29 Ma and standard deviation of 1.5, leading to a HPD 95% of 26.1–31.9 Ma, following the divergence times estimated in Datzmann, Helversen, and Mayer (2010).

We carried out three independent runs of 30 million generations for each set, and sampled trees every 1000 generations. Tracer 1.5 (Rambaut, Suchard, Xie, & Drummond, 2014) was used to check for convergence and for effective sample sizes (ESS) of parameters larger than 200. A maximum clade credibility tree was generated in TreeAnnotator after 20% of sampled trees were discarded as burn-in.

Demographic analyses

DNAsp 5 (Librado & Rozas, 2009) was used to calculate neutrality tests, Tajima's D (Tajima, 1989) and Fu's Fs (Fu, 1997), which were employed to infer demographic processes such as recent expansions.

We also estimated the variation of effective population size (Ne) through time for both main lineages of *G. soricina*, using the Bayesian Skyline Plot (BSP) analysis implemented in BEAST2. For both groups the GTR + G nucleotide substitution model was applied. The dates inferred in our divergence time analyses were employed as node calibration. We carried out three independent runs of 20 million generations each, and sampled trees every 1000 generations. The results were combined in LogCombiner for each population. The results were summarized and analysed in Tracer 1.5 (Rambaut et al., 2014).

Biogeographic analyses

The software Reconstruct Ancestral States in Phylogenies (RASP; Yu, Harris, & He, 2012) was used to reconstruct ancestral areas for the main lineages of *G. soricina*, based on methods where topological uncertainty is taken into account: Statistical Dispersal Vicariance Analysis (S-DIVA; Yu, Harris, & He, 2010) and Statistical Dispersion-Extinction-Cladogenesis Model (S-DEC; Beaulieu, Tank, & Donoghue, 2013). For both methods we used an entire posterior distribution of trees (comprising 15,000) generated on BEAST 2 and a maximum clade credibility tree generated on TreeAnnotator.

In order to infer ancestral ranges, we subdivided the distribution of *G. soricina* on the basis of sampled subspecies distribution range. Aiming to improve spatial resolution, we further divided Central and South America into two sub-regions each, which resulted in the following

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scheme of codes representing the areas: (A) North of Central America (Mexico, Guatemala, El Salvador), (B) Jamaica, (C) South of Central America (Panama and Nicaragua), (D) Western Andean regions of Peru and Ecuador, (E) North of South America, (F) Central and southern regions of South America. We avoided very distant disjoint ancestral areas by only allowing the following combination of areas: AB, AC, BC, ACD, ACE, ACEF, CD, CE, and CEF.

Results

Phylogeny and phylogeography

All phylogenetic analyses (MP, ML, and BI) based on concatenated mitochondrial genes yielded congruent topologies, revealing two monophyletic and statistically well-supported groups (Fig. 1 and S4, see supplemental material online). These phylogenetic groups coincide with mtDNA lineages of populations separated by the Andes, which are here called H1 and H2 (see Fig. 2). H1 is composed of the subspecies *G. s. handleyi*, *G. s. valens*, and *G. s. antillarum*, whose distribution comprises Mexico, Central America, and the Western Andean region of South America. H2 is composed of *G. s. soricina*, which is restricted to most of South America, east of the Andes. With the exception of *G. s. handleyi*, all subspecies were recovered as well-supported monophyletic groups.

Bayesian and MP analyses based on each marker separately yielded topologies congruent with the concatenated one. Monophyletic intraspecific lineages were corroborated by population genetic analyses (see below) and haplotype network (Fig. 2), where the H1 and H2 groups were also recovered.

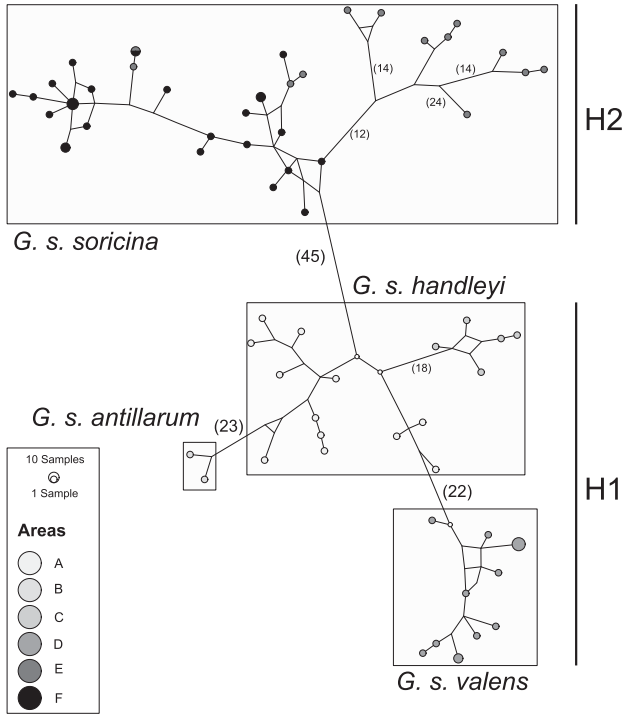

Fig. 2. Median joining Cyt b haplotype network. Numbers between parentheses indicate the number of mutations between haplotypes. For area code see Fig. 4.

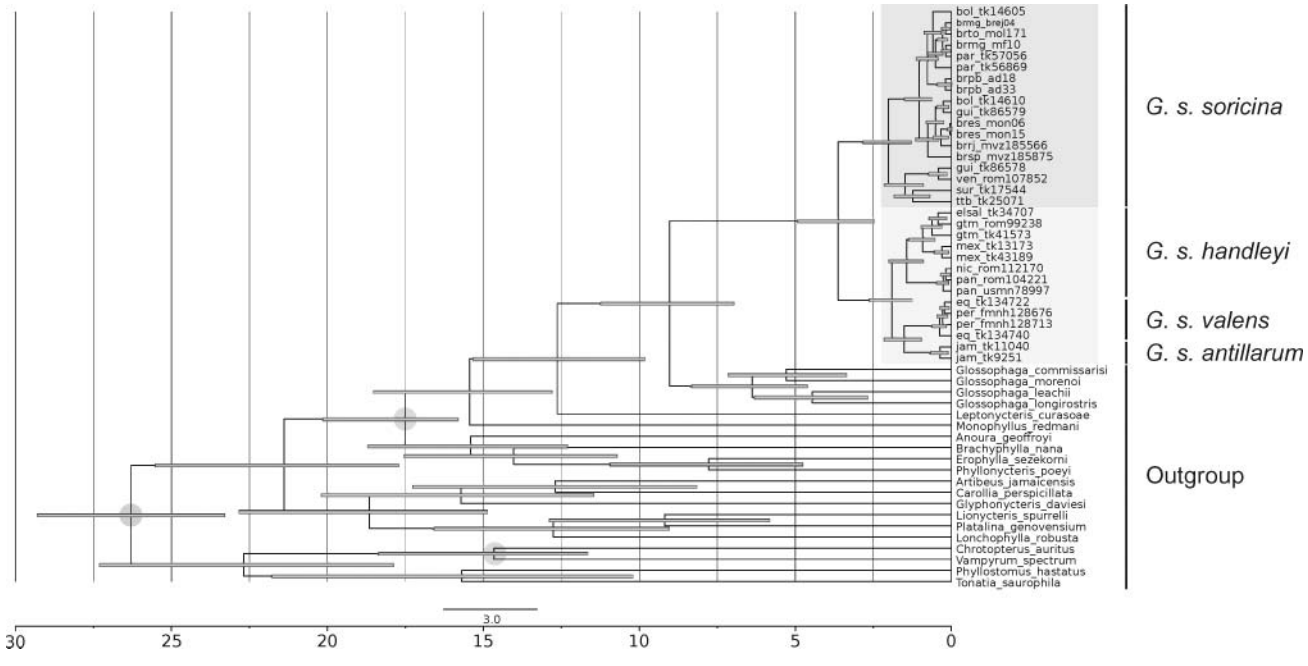

Fig. 1. Maximum clade credibility tree under UCLN model showing the divergence times between the main lineages in *G. soricina*. Horizontal axis represents time (in million years ago). 95% HPD interval of node ages are represented by grey horizontal bars. The grey rectangles highlight the two main lineages in *G. soricina*.

Table 1. Genetic distance amongst subspecies of *G. soricina* based on Cyt b data. Values below diagonal are distances between pairs of subspecies followed by their respective deviation. Underlined values between parentheses are average genetic distance inside each subspecies.

	G. s. soricina	*G. s. antillarum*	*G. s. handleyi*	*G. s. valens*
G. s. soricina	(0.02 ±0.002)	–	–	–
G. s. antillarum	0.062 ± 0.008	(0.008 ±0.002)	–	–
G. s. handleyi	0.057 ± 0.006	0.034 ± 0.005	(0.023 ±0.003)	–
G. s. valens	0.069 ± 0.008	0.036 ± 0.005	0.032 ± 0.004	(0.007 ±0.002)

Sequences characterization and variability patterns

For Cyt b we used 1062 bp in our analyses. Of these, 889 sites were constant and amongst the variable sites, 160 sites were parsimony-informative. Cyt b haplotype diversity was h = 0.995 ± 0.004 and nucleotide diversity was π = 0.041 ±0.001. For COI we used 632 bp, 552 sites being constant and 54 sites parsimony-informative. Diversity estimates for this marker were: h = 0.969 ± 0.008 and π = 0.023 ±0.001. DBY had 491 bp analysed and only three sites were parsimony-informative, which resulted in diversity estimates close to zero (h = 0.031 ± 0.03 and π = 0.00008 ± 0.0008). Despite the fact that we could not perform any further analyses based on DBY, we should note that from those three polymorphic sites, positions 22 and 134 had a T for *G. s. soricina* and an A for *G. s. handleyi*, respectively. These traits seem to be specific to each group, being treated as molecular synapomorphies when mapped in a phylogeny.

Estimated genetic distance amongst subspecies (see Table 1) based on Cyt b ranged from 0.032 ± 0.004 between *G. s. handleyi* and *G. s. valens*, to 0.069 ± 0.008 between *G. s. soricina* and *G. s. valens*. In fact, the distances between *G. s. soricina* (member of H2) and any other subspecies (members of H1) are the largest ones, which makes *G. s. soricina* the subspecies most genetically divergent. We had only two subspecies sampled in our COI dataset, *G. s. handleyi* and *G. s. soricina*. The estimated genetic distance was 0.043 ± 0.007, which was up to almost 10 times the average distance inside each subspecies (S1, see supplemental material online).

Corroborating previous results, AMOVA yielded elevated Φst values for both markers (Table 2). It indicates the existence of geographically structured populations, probably related to a limited gene flow between Cis- and Trans Andean regions.

Divergence time analyses

While the Bayes factors test allowed us to discard a strict clock hypothesis (see Supplemental material S1), models differing in the use of the age of *Palynephyllum* for node calibration, either as Glossophaginae or a Lonchophyllinae, were not statistically different. Therefore we followed Czaplewski et al. (2003) and opted for the model in which the age of *Palynephyllum* was used as a calibration for

Table 2. Summary of population genetics analyses based on Cyt b and COI. Underlined Φst, D and Fs values represent significant values. N = sample size; H = haplotypes; h = haplotype, diversity; π = nucleotide diversity; D = Tajima's D; Fs = Fu's Fs.

Source of variation	Φ_{ST}	N	H	h	π	D	Fu's Fs
Cyt b							
subspecies							
G. s. antillarum	0.675	2	2	–	–	–	–
G. s. handleyi		18	18	1.000 ±0.018	0.026 ±0.01	−0.53	−4.511
G. s. soricina		37	30	0.989 ±0.008	0.02 ±0.01	−0.88	−6.013
G. s. valens		14	10	0.923 ±0.060	0.02 ±0.02	−0.17	−1.317
regional groups							
H1	0.645	33	29	0.986 ±0.0135	0.024 ±0.012	−0.11	−6.232
H2		39	34	0.991 ±0.008	0.021 ±0.010	−0.733	−10.397
COI							
regional groups							
H1	0.775	32	15	0.824 ±0.06	0.004 ±0.002	−1.643	−6.243
H2		68	37	0.970 ±0.007	0.011 ± 0.006	−1.221	−17.068

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Glossophaginae diversification. The divergence between the groups H1 and H2 (Fig. 1 and node A S4, see supplemental material online) was estimated to have occurred between ~2.4 and 5 Ma (Fig. 1). The diversification of the subspecies of H1 group seems to be restricted to the Pleistocene, while *G. s. soricina* lineage, possibly, seems to exist since the late Pliocene.

Demographic analyses

Although in most cases we found non-significant Tajima's D values, Fu's Fs was negative and significant for both H1 and H2 and at least one subspecies of each group (Table 2). These results may indicate recent population expansion, and are corroborated by the high h and low π registered for both markers.

In accordance with neutrality test results, BSP based on Cyt b revealed demographic expansion in both groups of *G. soricina* (Fig. 3) between ~0.25 Ma and 0.20 Ma, a period characterized by a relative increase in average global temperature (Bintanja & Wal, 2011). While H2 (*G. s. soricina*) keeps its pattern of demographic expansion to the present, H1 subspecies presents stable effective sizes (Ne) from ~0.1 Ma to 0.03 Ma, when it undergoes a slight decrease.

Biogeographic analyses

Both S-DIVA and S-DEC returned congruent results. Despite differences in ancestral areas probability, most probable ancestral areas were the same, in most cases, for the main lineages of *G. soricina* (Fig. 4).

Our results suggest that the *G. soricina* ancestor showed a wide distribution (CEF, Fig. 4), ranging from Central America to southern South America (east of the Andes). From this ancestral area CEF, *G. soricina* would have dispersed into other areas (A, B, and D), and subsequently would have experienced vicariant events that led to the disjunct distribution currently observed (ACD, B, and EF).

Jamaica colonization is inferred as the result of a recent dispersal of ancestral populations which originated from Central America. Despite the results pointing to Central America as the most probable ancestral area, we cannot exclude Mexico (A, AC, and ACD) as a possible candidate.

When we consider the colonization of area D (Western Andean region of South America), the methods employed disagree with respect to the extension of the ancestral area. S-DIVA suggests AC as the most probable ancestral area, while S-DEC suggests C as the most probable ancestral area. However, both methods suggest that dispersion is the most likely mechanism behind the occupation of area D.

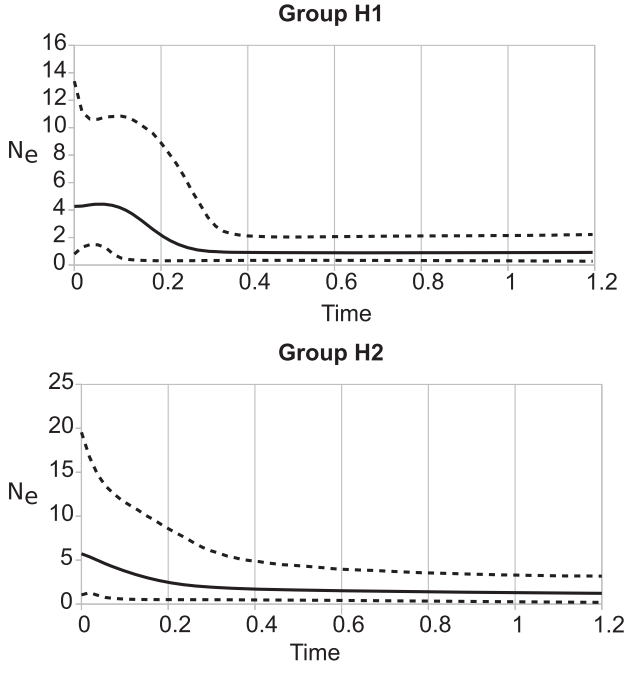

Fig. 3. Past demographic dynamics for both groups of *G. soricina* (H1 and H2). Dashed lines represent HDP 95% interval.

Discussion

Phylogeny, phylogeography, and genetic diversity

The different approaches employed in this study (phylogenetic, phylogeographic, biogeographic, and population genetics) showed consistent results for the markers used, thus confirming the existence of two main lineages in *G. soricina*, therefore corroborating the results of previous works (Clare, 2011; Ditchfield, 2000; Hoffman & Baker, 2001).

The elevated haplotype diversity values associated with low nucleotide diversity values are consistent with the expected pattern for a more vagile species, such as *G. soricina*, which can fly up to 60 km in one night (Helversen & Reyer, 1984). This pattern can also be observed in the haplotype network, where haplotypes of individuals from different countries are separated by just a few mutation steps. There is even an extreme case where individuals sampled in locations ~1500 km distant from each other share the same haplotype (see supplemental material S3).

At first glance, these results indicating high gene flow seem to disagree with the elevated Φ_{ST} values that suggest population structure. However, it is important to note that these Φ_{ST} values reflect the divergence between the two major groups, H1 and H2, whose genetic distance is equal to, or greater than, three times the distance within subspecies, or twice the distance amongst subspecies of the same group. Also, as will be discussed later, these groups

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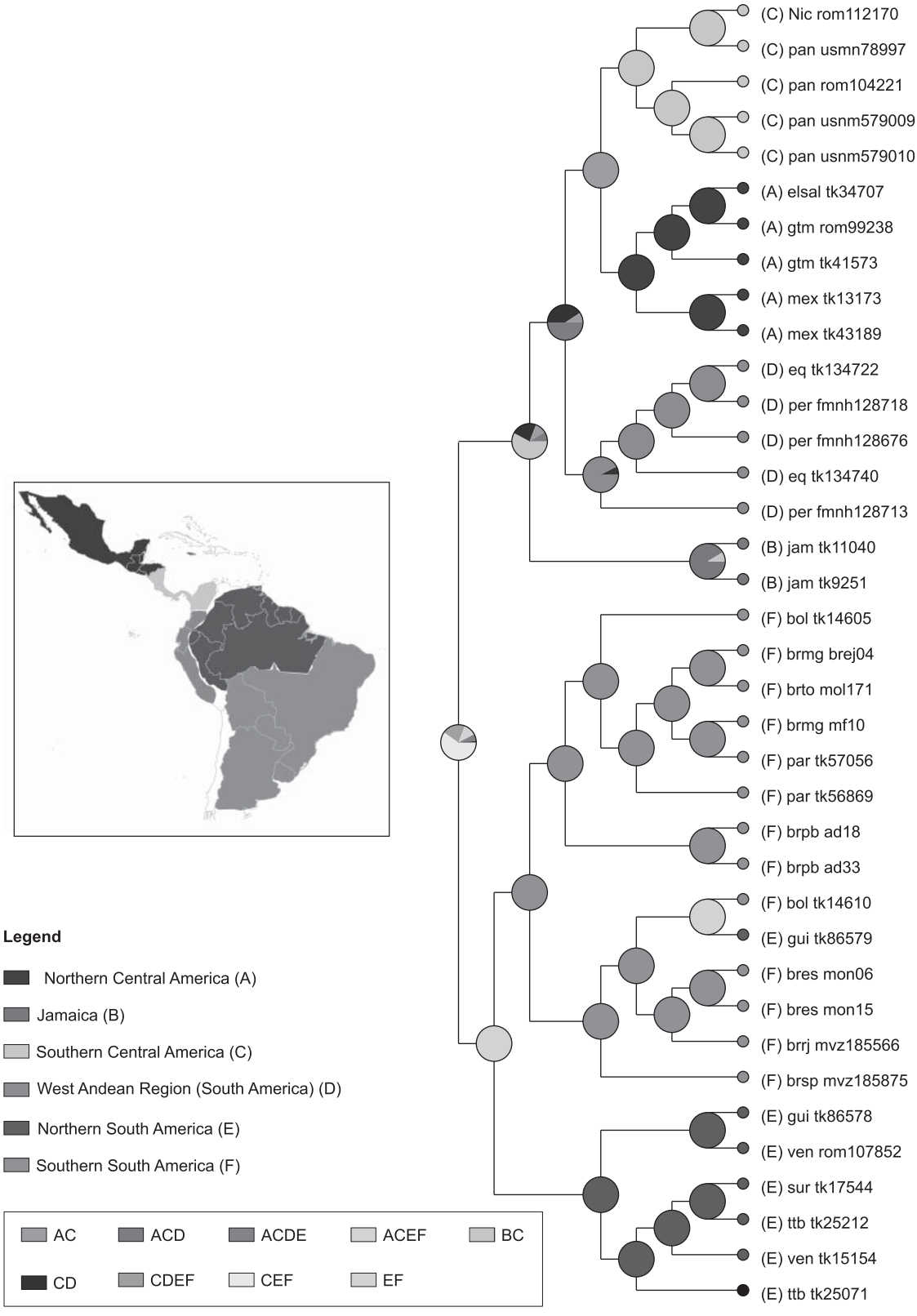

Fig. 4. S-DIVA biogeographic reconstruction (only topology shown) for *G. soricina*. Each sample was assigned to one of the following localities: A = Mexico, Guatemala, El Salvador; B = Jamaica; C = Panama, Nicaragua and Costa Rica; D = South America west of the Andes; E = Northern South America and east Andean Amazon; F = South America: east of Andes and south of Amazon region.

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appear to be allopatric, thus explaining the high Φ_{ST} values. Allied with this is the fact that both H1 and H2 are recovered as monophyletic groups for most of the phylogenetic reconstruction methods or datasets employed in this work. Another line of evidence pointing to the fact that *G. soricina* is composed of two lineages evolving independently is the haplotype network, where H1 and H2 are separated by more than 48 mutation steps, which is more than twice the greatest number of mutations separating subspecies within a group.

Divergence times and biogeography

Our results indicate that the divergence between H1 and H2 (node A, S4, see supplemental material online) occurred between ~2.4 and 5 Ma. For this period, some authors (Gentry, 1982; Gregory-Wodzicki, 2000; Mora et al., 2008; Simpson, 1979) suggest that orogenic events would have occurred, being responsible for shaping the current altitudinal configuration of the Colombian Andes. In this Andean region, until the late Miocene and early Pliocene, elevations in the Eastern Cordillera were estimated to be no more than half of their current values, but since ~5.4 Ma the elevation has increased rapidly, reaching modern elevations (~4000 metres above sea level (asl) in the eastern flank) by ~2.7 Ma (Gregory-Wodzicki, 2000; Mora et al., 2008). These events could have led populations of *G. soricina* to a disjunct distribution, thus creating a barrier that drastically reduced the gene flow between Cis- and Trans-Andean populations. We suggest that this could have been a physical barrier, originating from the Eastern Cordillera uplift itself since this event led to the formation of Cis- and Trans-Andean ecosystem components (Horton et al., 2010). We believe that, despite being older, the Western and Central Cordillera alone do not represent geographic barriers capable of preventing gene flow between populations of *G. soricina* from Central and South America, since their northern regions, located on the Colombian department of Córdova, present a low elevation profile (< 1000 m asl).

As a result, we suggest that allopatric divergence of these populations has resulted in the independent lineages H1 and H2 currently observed. This scenario is supported by the results of our biogeographic analyses that suggest a vicariant event as the cause of the current disjunct distribution of populations from southern Central America and South America (east of the Andes).

However, vicariance does not explain current distributions of all subspecies. *Glossophaga soricina valens* (restricted to western Andean region of South America) seems to have originated from populations of *G. soricina* that dispersed along the Pacific coast of Central America to occupy the western Andean region of South America. Another case where dispersion appears to be the key element to explain the current distribution is the colonization of Jamaica. It possibly took place between ~0.9 and 2.2 Ma (time estimated for the divergence between *G. s. antillarum* and the other subspecies of H1 group). It is a period marked by significant changes in relative sea levels, when it was ~80 m lower than the current level (Bintanja & Wal, 2011). These results support the hypothesis of Baker and Genoways (1978), which suggests that *G. soricina* would have come out from Yucatan (Mexico) and arrived at Jamaica at a time when the sea level was lower than the current one.

Demography

BSP analyses and neutrality tests indicate events of demographic expansion that begin between 0.20 and 0.25 Ma for both groups, after remaining stable for a long period, and extend to the present. These results suggest that Pleistocene climatic fluctuations (Bintanja & Wal, 2011) seem to not have significantly affected the population size and structure in *G. soricina.* However, other Neotropical bat species that show preference for forested areas were shown to be influenced by Pleistocene climatic cycles (Martins, Templeton, Pavan, Kohlbach, & Morgante, 2009; Pavan et al., 2011). This can be explained by the fact that *G. soricina* is a generalist and tolerant species, and can be found in many different habitats, including rural areas and urban centres (Esbérard, 2003; Luz, Costa, Lourenço, & Esbérard, 2011; Perini, Tavares, & Nascimento, 2003; Reis & Peracchi, 1987). As discussed by Peres et al. (2015), the effects of climate fluctuations tend to be more pronounced in species associated with a particular vegetation type.

Taxonomic considerations

The molecular patterns discussed here strongly suggest that an elevated divergence amongst *G. s. soricina* and the other subspecies seem to be reflected in morphological traits of this subspecies. According to Webster (1983), *G. s. soricina* can be easily distinguished from all the other subspecies. The author also enumerates some traits that justify his point of view: *G. s. soricina* is the smallest subspecies; its pelage is darker, its rostrum is short and narrow, it presents a moderate rostral slope, and it has a subparallel zygoma (Webster, 1983). As previously noted by Hoffman and Baker (2001) and Clare (2011), there is a strong possibility that we may be facing a case of cryptic species.

Not all subspecies, however, find support on phylogenetic or phylogeographic analyses. That is the case of *G. s. handleyi*, which was not recovered as a monophyletic group in any of the analyses performed in this study. It was, instead, recovered as a polyphyletic group, whose history cannot be separated from other subspecies of the

H1 group, and whose relations could not be resolved by the analyses based on the markers employed in this work. Since the validity and biogeographic history of *G. s. handleyi* requires additional scrutiny, we suggest that its status should be revised, especially considering the validity of the taxon and its relationship to other clades within *G. soricina*.

Final considerations

We found that Quaternary climatic fluctuations had little effect on past population dynamics in *G. soricina*, unlike some other widespread species of neotropical bats (e.g. Ditchfield, 2000; Martins et al., 2009; Pavan et al., 2011). As mentioned before, this is possibly related to the factors promoting its broad geographic range, such as the generalist and tolerant aspects of its ecology, which makes this species less prone to isolation by the rising of ecological barriers associated with the forest retraction during glacial periods. This corroborates the ideas of Jablonski and Roy (2003) and papers cited therein. We also found that events that caused large scale physiographical changes (e.g., Andes uplift and sea level oscillation), are probably the main drivers of the diversification patterns we currently observe in *G. soricina.*

Considering this study case involving *G. soricina* and its patterns of diversification, we suggest that geographic and/or climatic events that cause physiographic changes are more likely to create barriers to the gene flow amongst populations of species with broad geographic range. Our results corroborate the idea that the Andes uplift played an important role in the evolution of Neotropical biodiversity (De-Silva, Elias, Willmott, Mallet, & Day, 2016; Weir, 2011), and, in this context, this study represents a contribution to the understanding of the processes that drove diversification in the Neotropics.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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Supplemental data

Supplemental data for this article can be accessed at http://dx.doi.org/10.1080/14772000.2016.1271060.

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