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Short Communication

Genetic diversity of the swamp rat in South America: Population expansion after transgressive-regressive marine events in the Late Quaternary

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ABSTRACT

We examined the phylogeography of the South American swamp rat *Scapteromys tumidus* using complete mitochondrial DNA cytochrome b sequences. This species is endemic to the Pampas biome and lives near the coastal plain but also in inland continental areas. The coastal domain of such region experienced a highly dynamic geological history. The inland fraction is part of Precambrian and Mesozoic spills and sedimentary basins, while most of the coastal plain was shaped by transgressive-regressive marine events in the Late Quaternary. As fluctuations in the sea level during this period produced large lateral displacements of the shoreline, originating four barrier–lagoon systems that shaped the present coastline, continental area significantly increased from this time. We hypothesized that the *S. tumidus* have expanded its range from that period, ramped by its adaptive ability to humid areas. Thus, we examined whether historical Pleistocene events had affected genetic variation of this species along its distributional range. Bayesian phylogenetic analysis and the haplotype network inferred two major genetic clusters along the distribution of *S. tumidus*. Neutrality tests suggest that populations experienced demographic changes and Bayesian skyline plot evidenced a marked recent demographic expansion pattern, intensified from 350 to 300 kya. Such date coincides with the formation of the lagunar barrier II (dated to ca. 325 kya) and the concurrent initial formation of the coastal plain and increase in continental area.

The influence of Quaternary climate and geological changes on the extant diversity of Neotropical species has been recurrently studied in South America organisms from a tropical systems perspective, in which a retraction into refugees is commonly proposed (Carnaval and Moritz, 2008; Carnaval et al., 2009; Haffer, 1969; Porto et al., 2013; Vanzolini and Williams, 1981). In contrast, open areas such as the Pampas overall present a distinct model in relation to tropical systems, such as an expansion due to low temperature and dry conditions during the Pleistocene (see Turchetto-Zolet et al., 2013). Phylogeographic studies in this system, dealing with different organisms (e.g. rodents [Lopes et al., 2013; Mapelli et al., 2012; Montes et al., 2008; Mora et al., 2013; Palma et al., 2012], plants [Fregonezi et al., 2013; Longo et al., 2014; Mäder et al., 2013], lizards [Felappi et al., 2015] and Patagonian fauna and flora [Sérsic et al., 2011]), unravel contrasting patterns in regional and local scales.

Population genetic structure is determined not only by micro evolutionary processes (as genetic drift and natural selection), but also via its complex interaction with ecological parameters, including population size and migration (Allendorf and Luikart, 2012). Thus, explore genetic variation in species presenting conspicuous ecological traits, such as habitat preference, is suitable to infer

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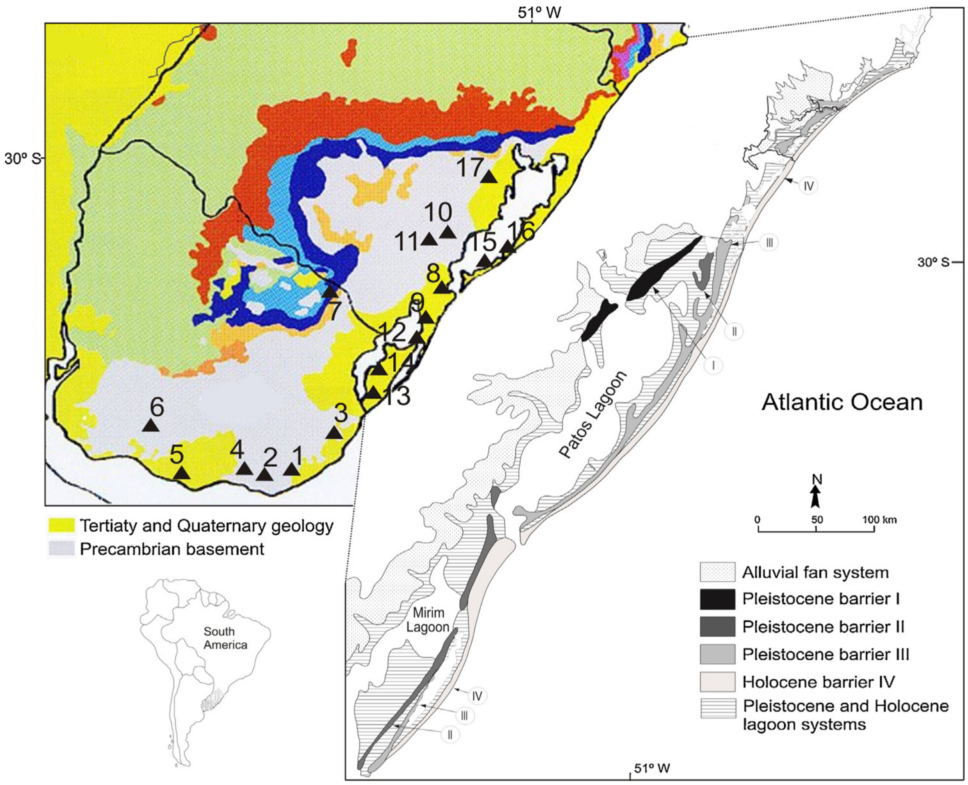

Fig. 1. Collecting localities of *Scapteromys tumidus*. Numbers correspond to sites showed in Table 1. Coastal plain is shown in detail to depict the four barrier stages.

demographic changes during glacial and interglacial cycles in the Neotropics.

The swamp rat *Scapteromys tumidus* (Waterhouse 1837) is endemic to the Pampas grassland biome (Overbeck et al., 2007), distributed in the southernmost Brazil (Rio Grande do Sul State [RS]) and entire Uruguay (D'Elía and Pardiñas, 2004; Freitas et al., 1984; Musser and Carleton, 2005). This species occupy habitats near wetland vegetation (wet meadows, reeds, *Typha* and *Eryngium* stands) (Barlow, 1969; González and Martinez-Lanfranco, 2010) and watercourses, such as swamps, ponds, small creeks, and large rivers (D'Elía and Pardiñas, 2004). *Scapteromys tumidus* is semi-aquatic, as it presents morphological traits to swim (Massoia and Fornes, 1964), as well as to climb trees, a behavior reported as an adaptation to live in flooded areas (Barlow, 1969; Sierra de Soriano, 1969). Currently, this species occupies both coastal and inland areas, along a wide range.

Demographic history and biogeography might have had an essential role in outline the genetic variation of populations (D'Elía and Pardiñas, 2004). The coastal domain of such region experienced a highly dynamic geological history. The inland fraction is part of Precambrian and Mesozoic spills and sedimentary basins, while most of the coastal plain was shaped by transgressive-regressive marine events in the Late Quaternary. As fluctuations in the sea level during this period produced large lateral displacements of the shoreline, originating four barrier–lagoon systems that shaped the present coastline (Fig. 1), continental area significantly increased from this time. We thus hypothesized that the swamp rat might have expanded its range by colonizing new available areas, increasing effective population size from the Late Quaternary. Long periods of population stability, or, alternatively, the recent colonization of new habitats have contrasting effects on the pattern of spatial apportionment of genetic variation at local and regional levels (Matocq et al., 2000; Slatkin, 1993; Wlasiuk et al., 2003). Thus, herein we characterize patterns of genetic variation in populations of *S. tumidus* across its distributional range in the Pampas biome, in order to evaluate the phylogeographic structuring of populations. Based on complete mitochondrial cytochrome b sequence haplotypes we inferred past demographic changes and addressed to what extent geological and historical factors have shaped the current distribution of the swamp rat, and might have influenced intraspecific patterns of variations.

A total of 131 specimens of *S. tumidus* (114 field-collected from 2010 through 2012, and 17 incorporated from database), from 17 localities, covering the whole species distribution, were surveyed (Fig. 1 and Table 1). Genomic DNA was isolated from tissue samples (liver and/or muscle) using the CTAB method modified from Doyle and Doyle (1987). The complete cyt *b* (1146 bp) gene was amplified through Polymerase Chain Reaction (PCR) using primers MVZ05 and MVZ14, following conditions described by Smith and Patton (1993). PCR aliquots were checked on 1% agarose gel stained with GelRed (Biotium Inc., Hayward, CA, USA). The remaining products were purified with Exonuclease and Shrimp Alkaline Phosphatase (GIBCO-BRL Life Sciences/Invitrogen, Carlsbad, CA, USA), and sequenced at Macrogen, Inc., Seoul, Republic of Korea, with the same primers used in the PCR. Forward and reverse sequences were aligned and cross-checked to resolve ambiguities. Fifteen new haplotypes were deposited in GenBank under the accession numbers KP233846-60 (Table 1).

Multiple sequence alignments were performed using Codon Code Aligner (CodonCode Corp., USA), and inspected manually. Measurements of mtDNA diversity, including the mean number of pairwise differences (Nei, 1987), definitions of haplotypes, and haplotype diversity, and Neutrality tests (Tajima's *D*, Fu and Li's *D* and *F*, Fu's *FS*) were calculated in the program DNASP 5.0 (Librado and Rozas, 2009). A median joining haplotype network (Bandelt et al., 1999) was constructed in NETWORK 4.6 (http://www.fluxus-engineering.com/sharenet.htm). Levels of genetic structure among subpopulations was characterized using ϕ_{ST}, which is analogous to Wright's *F*-statistics but takes into account the genetic distance among haplotypes using ARLEQUIN 3.5 (Excoffier and