



Geography and past climate changes have shaped the evolution of a widespread lizard from the Chilean hotspot



Carla Muñoz-Mendoza^a, Guillermo D'Elía^b, Alejandra Panzera^{a,c}, Marco A. Méndez T.^d, Amado Villalobos-Leiva^a, Jack W. Sites Jr.^e, Pedro F. Victoriano^{a,*}

^a Departamento de Zoología, Facultad de Ciencias Naturales y Oceanográficas, Universidad de Concepción, Casilla 160-C, Concepción, Chile

^b Instituto de Ciencias Ambientales y Evolutivas, Universidad Austral de Chile, Campus Isla Teja s/n, Valdivia, Chile

^c Doctoral Program in Systematics and Biodiversity, Facultad de Ciencias Naturales y Oceanográficas, Universidad de Concepción, Concepción, Chile

^d Facultad de Ciencias, Universidad de Chile, Santiago, Chile

^e Brigham Young University, Provo, UT, USA

ARTICLE INFO

Keywords:
Climate change
Liolaemus
Chile
LGM
Phylogeography

ABSTRACT

The complex orogenic history and structure of Southern South America, coupled with Pleistocene glacial cycles, have generated paleoclimatic and environmental changes that influenced the spatial distribution and genetic composition of natural populations. Despite the increased number of phylogeographic studies in this region and given the frequent idiosyncratic phylogeographic patterns, there is still the need to focus research especially on species that are currently distributed within a wide range of bioclimatic regimes, and that historically have been subject to contrasting scenarios. *Liolaemus tenuis* is a widely distributed lizard species inhabiting latitudinally in almost 1000 km through central and southern Chile. Here we describe the geographical patterns of genetic variation and lineage diversification within *L. tenuis*, and their association with geography and Pleistocene glaciations, using sequences from one mitochondrial and two nuclear genes, and five microsatellite loci, and covering most of the species distributional range. Our results revealed a high diversity both within and among populations, as well as two phylogeographic breaks, which are consistent with two of the larger rivers of central Chile, the Maipo and Biobío Rivers. *Liolaemus tenuis* is characterized by several allopatric lineages, especially in its north and central range, which suggest a history of multiple vicariance processes. Conversely, populations found in the southern range, south of the Biobío River, show signatures of recent decreases in effective population sizes, coupled with recent range expansions and secondary contact. Niche “envelope” data are consistent with patterns of genetic variation; both suggest a history of discontinuous areas of relatively stable populations throughout all of the distribution of *L. tenuis*. These data are also consistent with higher probabilities of habitat suitability north of the Maipo River (ca. 33°S), in both coastal areas and the “Intermediate Depression” between 34° and 37°S, as well as in the southern Coastal Cordillera between the Biobío and Araucanía regions. Interestingly, both molecular and niche envelope modeling data suggest that some populations may have persisted in fragmented refugia in Andean valleys, within the limits of the ice sheet. Finally, our results suggest that several populations of *L. tenuis* colonized glaciated regions from refugial areas in lowlands and coastal regions, and in the southern distribution, historic migration events would have occurred from refugial areas within the limits of the ice sheet.

1. Introduction

Geological events, coupled with past climatic changes have played a key role in shaping current patterns of genetic diversity (Hewitt, 1996). Temporal and spatial environmental heterogeneity are among the main drivers of intraspecific differentiation (e.g., Levy et al., 2012; Wang and Yan, 2014) and ultimately of species diversification (e.g., Brown et al., 2014). Consequently, a positive association between habitat

discontinuity (e.g., landscape roughness and/or the occurrence of barriers) and beta levels of intraspecific diversity (population genetic structure and/or structured lineage distribution) is expected. For example, several studies have shown the importance of large rivers acting as barriers to gene flow and delimiting the distributions of closely related subspecies or species of tropical birds (Capparella, 1991; Cheviron et al., 2005; Maldonado-Coelho et al., 2013; Ribas et al., 2011; Smith et al., 2014; Voelker et al., 2013), lizards (Pellegrino et al., 2005;

* Corresponding author.

E-mail address: pvictori@gmail.com (P.F. Victoriano).

<http://dx.doi.org/10.1016/j.ympev.2017.08.016>

Received 6 January 2017; Received in revised form 22 August 2017; Accepted 24 August 2017

Available online 05 September 2017

1055-7903/ © 2017 Elsevier Inc. All rights reserved.

Torres-Pérez et al., 2007), and mammals (Link et al., 2015; Nicolas et al., 2011; Patton and da Silva, 1998). In the same context, historically restricted stable habitats, which allow populations to remain in place over time, are positively correlated with high levels of intrapopulation genetic variability and demographic equilibrium. The opposite situation is expected for areas that have been repeatedly exposed to climatic fluctuations, as the Pleistocene glaciations, during which populations exhibit signatures of recent colonization and demographic expansion suggested, due to, for example, a lack of mutation-drift equilibrium and high historical levels of gene flow (e.g., Ding et al., 2011; Zhang et al., 2008a, 2008b).

One example of dynamic and heterogeneous scenario is western temperate South America, where the uplift of the Andes and Pleistocene glaciation cycles would have had important evolutionary consequences for the biota. The Andes, whose uplift started approximately 23 million years ago, have acted as a barrier between the current western slope and the Argentine Patagonia, and have shaped a high topographic heterogeneity along the western slope (Gregory-Wodzicki, 2000). This orogenic event history would have facilitated evolutionary diversification, ultimately forming much of the biota to what is now referred to as the “Chilean Biodiversity Hotspot” (Antonelli et al., 2010; Myers et al., 2000).

Along the north-south axis of the western Andean range, there is a pronounced altitudinal gradient, which is characterized by high altitudes and more heterogeneity in relief from south to north. This topographical gradient is also characterized by an increasing latitudinal gradient of fragmentation of the Chilean “lowlands” that lay between the Andes and the Pacific Coastal Cordillera (Fig. 1). The opposite topography is observed in the Andean Cordillera as it extends to the south; overall elevations are lower and intervening valleys are more connected.

Over this orogenic history, and interacting with it, four Pleistocene climatic events occurred that had important demographic consequences (McCulloch et al., 2000; Rabassa and Clapperton, 1990; Ruzzante et al., 2008). Such cycles had a greater impact along the southern Andes. During the Last Glacial Maximum (LGM) the ice sheet coverage increased in extension towards the south, also extending onto low altitude areas (Hulton et al., 2002; Markgraf et al., 1995; Villagrán, 1991; Villagrán et al., 1995). In the western slope of the Andes in Central Chile, the northern limit of the ice sheets reached approximately the latitude of 33°S at high Andean regions and covering all the land up to the Pacific Coast south of the 42°S. According to this, the coastal mountain range, as well as coastal areas north of 41°S, would have constituted stable areas where species would have survived during the LGM (Armesto et al., 1994; Sérsic et al., 2011; Villagrán, 2001; Villagrán et al., 1995). As such, in the western slope of the Andes the intensity of the glacial effects on the biota would have increased towards the south (Amigo and Ramírez, 1998; Heusser, 2003; Smith-Ramirez, 2004), reducing effective population sizes (N_e) mainly in Andean and Southern populations (e.g., Lessa et al., 2010; Vera-Escalona et al., 2012; Victoriano et al., 2008).

Another distinctive feature of Chile is the series of parallel steep, high gradient, east-to-west flowing rivers (e.g., Aconcagua, Maipo, Maule, Biobío). These rivers may also act as barriers to gene flow structuring intraspecific genetic diversity in Chilean vertebrates and plants (Chesser, 1999; Lambrot et al., 2003; Sallaberry-Pincheira et al., 2011; Torres-Pérez et al., 2007; Unmack et al., 2009; Vásquez et al., 2013; Viruel et al., 2014). Nevertheless, no study has formally evaluated the combined effect of rivers, topographic relief, and shifting climates (glacial advances and retreats) in structuring the intraspecific genetic variation/phylogeographic history of any Chilean species. The north-south axis of over 4000 km of the Chilean Andes, combined with its west-east elevational gradient (sea level to above 6000 m), coupled to multiple ice sheet glacial advances and retreats in addition to simultaneous increases in river water volumes due to melting ice, would have dramatically impacted terrestrial (as well as aquatic) communities

in this region. As such, widely distributed Chilean species constitute a good system to assess the joint effects of geographical complexity, glacial cycles, and fluctuating river volumes, on intraspecific population differentiation and phylogeographic structure.

Liolaemus is a highly diverse (ca. 250 species; Uetz et al., 2016) and widely distributed genus of South American lizards. *Liolaemus tenuis* (Duméril and Bibron, 1837) is a broadly distributed species that encompasses a latitudinal range of 1000 km, from the Chilean regions of Coquimbo (ca. 30°S) to Los Ríos (ca. 40°S; Fig. 1), with peripheral populations also present on some eastern Andean slopes in the Argentinean province of Neuquén. The altitude range of this species extends from sea level up to 1800 m (Donoso-Barros, 1966; Pincheira-Donoso and Nuñez, 2005; Victoriano et al., 2008), and occurs in distinct habitat types ranging from “Mediterranean” shrubland to sub-Andean forests (Di Castri, 1968). As such, the species distribution encompasses both stable and topographically heterogeneous areas in the north, as well as southern latitude landscapes that were impacted by Pleistocene glaciations. Victoriano et al. (2008) suggested that the microevolutionary history of *L. tenuis* was influenced by Pleistocene glacial cycles, but the inferred demographic changes were not dated, nor were the locations of putative stable areas (refugia) identified and subsequent colonization routes hypothesized.

The aim of this study is to evaluate the phylogeographic structure of *L. tenuis* across most of its distributional range in order to test the following predictions. (1) Populations that now occur in previously glaciated areas, mainly distributed in the Andes, will show genetic signatures of demographic expansion and lower levels of genetic structure and diversity than populations that occur in areas that were free of ice during glaciations. (2) During glacial advances, refugial areas would have been located near the Coastal Cordillera in the Southern range of *L. tenuis*, and post-glacial population expansions would have occurred in a predominantly northwest to southeast direction. (3) The east-to-west flowing rivers have acted as barriers to gene flow, shaping distribution genetic structure of clades along a north-south latitudinal arrangement.

2. Materials and methods

2.1. Sample collection

The study is based on 225 specimens of *Liolaemus tenuis* collected at 84 sites (Fig. 1). Of these, 145 specimens from 41 localities were taken from the study of Victoriano et al. (2008). The other 80 individuals were newly collected (between 2007 and 2012) at 45 localities. The new specimens were captured with collection permits granted by the Servicio Agrícola y Ganadero (authorizations SAG-1898 and SAG-4729). All captures were carried out according to the protocols approved by the Bioethics Committee of the Universidad de Concepción (Chile). Individuals newly collected were deposited in the collection of the Museo de Zoología de la Universidad de Concepción (MZUC).

Sampling sites were classified into three groups, corresponding to the main Chilean bioclimatic zones, as follows: (1) North (N), including localities north of the Maipo River, an area that corresponds to the dry Mediterranean bioclimate zone; (2) Central (C), including localities between the Maipo and Biobío rivers, which correspond to the mesic Mediterranean area; and (3) South (S), including localities south of the Biobío River, covering the wet Mediterranean area, which includes the Valdivian Forests (Di Castri, 1968; Table S1).

2.2. Laboratory procedures

Genomic DNA was extracted from muscle tissue using the commercial kit Wizard SV Genomic (Promega) following manufacturer's instructions. Detailed amplification and sequencing methods largely follow Broadley et al. (2006), Victoriano et al. (2008), and Portik et al. (2011a,b), and are available in Appendix A.

Download English Version:

<https://daneshyari.com/en/article/5592303>

Download Persian Version:

<https://daneshyari.com/article/5592303>

[Daneshyari.com](https://daneshyari.com)