# Chapter 10
# Phylogeography of Chilean Lizards: Histories of Genetic Diversification on the Western Slope of Southern Andes

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**Abstract** The western slope of the Southern Andes has complex orographic attributes and a dynamic paleoclimatic history, which seems to have been the driver of a great intraspecific genealogical diversification of lizards. Phylogeography tries to explain the spatial current patterns of genetic variation and genealogical intraspecific diversity, alluding to the features and the history of geographical scenarios. Although the number of these studies for South America is still low, the contributions that have emerged in recent years about the intraspecific diversification of reptiles in Chile have begun to sketch interesting hypotheses about the geographical factors that have likely contributed to the distribution of their genetic diversity. Such studies have focused mainly on species of the genus *Liolaemus*, the one with the highest levels of squamate species richness in southern South America. In West Austral Andes, a large part of the herpetofaunal diversity is concentrated in the Mediterranean and northern areas of the temperate forest, where several species are characterized by wide geographical ranges across varied environmental conditions. The general evidence indicates that the Chilean lizards have acquired high levels of genetic variability, coupled with complex geographic distributions and high levels of evolutionary differentiation, associated with landscape features, such as rivers and mountains. These influences have been further impacted by the interaction with dramatic past climate changes. Estimates based on mtDNA suggest that some of the species diversified during the Pleistocene (e.g., *L. tenuis* and *L. pictus*). These species have likely been most impacted by glaciations, suggested by a greater number of population reductions and postglacial expansions at greater latitude and altitude. These and other species, however, also show considerable levels of divergence and the existence of cryptic diversity (e.g., *L. tenuis*, *L. pictus,* and *L. monticola*). These patterns suggest that there may be more than one species within those that until now have been considered single taxonomic entities. It is also interesting to detect cases

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of congruent diversification among co-distributed lizards. From a biodiversity conservation perspective, the allopatric distribution of lineages of deep divergence and the spatial arrangements of genetic diversity and singularity suggest the existence of valuable intraspecific conservation units, most of which would be unprotected and in areas exposed to important anthropogenic changes.

**Keywords** *Liolaemus* · Intraspecific conservation · Southern Andes · Population differentiation

## 10.1 The Phylogeographic Context and Lizards

Knowing the spatial arrangement of genetic diversity and understanding the geographic processes that have influenced its evolutionary dynamics is relevant for two main reasons. On the one hand, inquiring about the environmental factors that have influenced the genetic diversification within a species is a key issue in evolutionary biology, in order to understand, among other aspects, the mechanisms that prelude speciation events (interface between micro- and macroevolution). And on the other hand, intraspecific variation constitutes a real component of biodiversity, and its study when taken to the geographical context is fundamental to define the intrinsic conservation value of evolutionary units within species (Moritz 2002). This is also a necessary aspect to predict the negative consequences on the number and spatial distribution of intraspecific lineages that the alarming global changes in course will bring.

At the end of the 1980s, when population genetics and phylogenetics were already mature disciplines, Avise and collaborators proposed creatively merging both approaches to better understand the evolution of populations within the framework of the attributes of the geographical landscape (Avise et al. 1987). They took advantage of the synergism between both disciplines and coined the term phylogeography to refer to the study of the principles and processes that have influenced the geographical distribution of lineages, especially those within species (Avise and Walker 1998). Their contributions come from studying the distribution of genetic biodiversity, including the reconstruction of genealogies, to explain their origin and distribution based on the history of the geographical space (Fig. 10.1). In a certain way, it can be said that biogeography and phylogeography, having common interests, just differ fundamentally in their temporal scales and in the hierarchies of the biodiversity they address. In its performance, phylogeography also calls for other disciplines, such as population ecology, paleontology, molecular biology, and geology, among others, allowing an integrated interpretation of the processes that affected the diversification of populations. In this way, phylogeography interacts and generates complementary contributions with other disciplines, such as genetic ecology (Lowe et al. 2004) and landscape genetics (Manel et al. 2003). Phylogeography contributes with evidence and methods to other disciplines too.

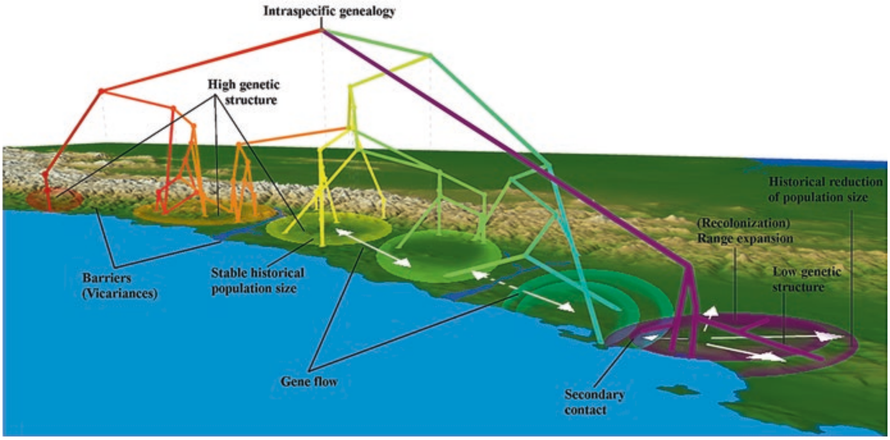

**Fig. 10.1** Intraspecific hypothetical genealogy projected on the geographical landscape and some of the patterns and processes analyzed in phylogeographic studies

The terms geogenomics and phylogeology were recently proposed as new subdisciplines of geology that integrate geologically relevant genetic evidence on a large scale, to test geological hypotheses (Acosta et al. 2014; Baker et al. 2014; Fritz and Baker 2017). In summary, phylogeography provides a great real and potential contribution to the knowledge of the history of Earth and in turn how and why populations have evolutionarily differentiated.

Despite the complexity of evaluating the role of spatial and temporal variations in the environment as promoters of intraspecific differentiation (Hewitt and Ibrahim 2001), two aspects are recurrent in the phylogeographic literature. On the one hand, the historical stability of habitat, understood as the degree of historical persistence of environmental conditions, seems to be an important factor for the herpetofauna, both at the intraspecific (e.g., Carnaval et al. 2009) and multispecies or community level (Werneck et al. 2012). On the other hand, the historical discontinuity of the habitat, with repercussions on population connectivity, would have functioned as an important diversification force (e.g., Bell et al. 2010). The interaction of both aspects would have influenced the formation of the spatial arrangements of the current genetic diversity, with responses dependent on the biology of each species (e.g., vagility, age of taxa, reproductive attributes, requirements, and tolerances). In this context, phylogeographic evidence suggests that areas that have long maintained their environmental conditions (e.g., climate and vegetation structure) have tended to harbor greater genetic variability and higher demographic stability, compared to scenarios that have drastically changed throughout time. In the case of habitats broken up by barriers, sometimes as archipelagos with small “islands,” these have contributed to population reduction events due to environmental change and should promote greater genetic differences between populations (structuring), with lower local diversity. In this sense, species of lizards that for a long time have existed along wide geographic ranges, with an interrupted geography and with different degrees of stability, should harbor complex spatial patterns of genetic diversification. This is the case of several species distributed in central-southern Chile, which is a territory with a high orographic heterogeneity and subjected to the effects of repeated glaciations (Heusser 2003).

Camargo et al. (2010) made an excellent review on the suitability of lizards as model species in evolutionary studies, given the knowledge about demographic aspects, life histories, and ecophysiology, among others. Although there are still considerably fewer phylogeographic studies for the Southern Hemisphere, they have increased since the 2000s (Beheregaray 2008), where herpetozoans are in an intermediate ranking, below mammals and plants, but above aquatic invertebrates and birds. In an interesting phylogeographic review of South America, Turchetto-Zolet et al. (2012) concluded that the herpetofauna includes species of old intraspecific divergences and with varied responses to glacial cycles, depending, for example, on the type of habitat (e.g., open or wooded). In this study, it is also clear that mitochondrial genes have been used in the majority of cases, and a smaller number of studies have included multilocus approaches. Recently, there have been works that incorporate NGS methods (massive parallel sequencing), although for lizards these still address phylogenetic relationships among multiple species, and the analysis in a phylogeographic context is still pending. For example, Panzera et al. (2017) recently published a phylogeny of *Liolaemus* species of the Chilean clade based on ultraconserved elements (UCEs), while Grummer et al. (2018) used a genomic approach for Patagonian species of the *Liolaemus fitzingerii* group. Although in Chile the greatest richness of lizard species extends from 23° S, in desert environments in the north, to 39° S in parts of the temperate forests in the south (Vidal et al. 2009; Vidal and Díaz-Páez 2012), a considerable diversity is concentrated in Mediterranean environments (Troncoso 2010). The total lizard richness in Chile comprises approximately 130 species, of which about 50% are endemic (Vidal and Díaz-Páez 2012) and 68 species are threatened (http://www.mma.gob.cl/clasificacionespecies/index.htm). The greatest lizard diversity of this part of South America is represented by species of the genus *Liolaemus*, an ecologically versatile and evolutionarily prolific group. Although still scarce, the phylogeographic literature suggests a complex and interesting history of diversification for these lizards. The objective of this chapter is to give a general view about the patterns and processes of intraspecific evolutionary diversification of lizards from central-southern Chile, based on the phylogeographic information published up to now, and to give some guidelines for future investigations in this field.

## 10.2 The Chilean Scenario

The Andes mountain range, which extends for more than 7000 km, constitutes the longest mountain chain on the planet (Ceccarelli et al. 2016). Although its beginnings go back to the Paleozoic (Ramos and Alemán 2000), its uplift would have been accentuated approximately 23 Ma, reaching a relief with heights similar to the current ones about 5 Ma. The extravagant and singular geography of central-southern Chile extends on the western slope of the Southern Andes (approx. 30° S–43° S), forming part of the Mediterranean Province from Santiago to the rainy Valdivian Forest, according to Morrone (2015). This part of South America has been a scenario with important evolutionary repercussions on its biota (Sérsic et al. 2011), where, compared to other mountain systems of the world, the role of physical factors such as temperature, rainfall, and relief seems to have been the most relevant in the processes of biological diversification (Antonelli et al. 2018). The most obvious effect was the East-West divide, which would have led to a marked differentiation between the biota of its Pacific slope and that of Argentine Patagonia, and in part was one of the mechanisms that generated the endemism in what is known as the Chilean hot spot of biodiversity (Myers et al. 2000). In the west, a series of latitudinally arranged basins added numerous interrupted areas, also distributed along a pronounced climatic gradient, and are being able to promote transverse speciation processes as found by Wallis et al. (2016) in the Alpine range. This arrangement of speciation could be one of the responsible factors for latitudinal endemism and a high phylogeographic differentiation within the western slope of the Southern Andes. For these reasons, central-southern Chile constitutes a privileged scenario to test phylogeographic hypotheses, with attributes of a great natural laboratory.

### *10.2.1 Chilean Physiography and Climatic Gradients*

Although it is not reasonable to refer to the phylogeographic space in geopolitical terms, in the case of Chile it is a minor problem, due to the high concordance between its territorial limits and its natural barriers. Its physical attributes facilitate in some way the prediction of expected phylogeographic patterns and the proposal of hypotheses about their causes. The main physiographic units of central-southern Chile are the Cordillera de la Costa, close to the Pacific Ocean, and the Cordillera de los Andes, both mountainous systems oriented latitudinally in a parallel arrangement and unconnected along a large part of their distributions. The intermediate depression or inner valley is located between these two mountain ranges, which forms an almost continuous flat area between 34° 30′ S and 37° 30′ S (Fig. 10.2a). This is a narrow scenario arranged vertically on the map, with a marked isolation imposed by the Andes to the east, the Pacific Ocean to the west and south, and the desert to the north. The Chilean relief shows interesting altitudinal gradients, both longitudinally (from the Andes to the Pacific coast) and latitudinally (Fig. 10.2b). For example, at the latitude of Santiago (33° S), mountains that exceed 4000 m are frequent, and valleys are often interrupted by transverse ranges that connect the Andes with the coastal mountain range. Toward the south, the mountains decrease in altitude, increasing the connectivity between low-altitude environments. Consistent with this geographical trend, the Andes gradually weakens as a barrier toward the south, which would have allowed greater historical communication between populations of the Patagonian and Pacific slopes. There is phylogeographic

**Fig. 10.2** (**a**) Major bioclimatic zones of Chile (based on Di Castri 1968). (**b**) Swath profiles showing rainfall and topography in west Southern Andes (based on Strecker et al. 2007)

evidence for this, as is the case of some freshwater fish (Muñoz-Ramírez et al. 2014; Ruzzante et al. 2006). This is also consistent with the presence of lizard species shared between Chile and Argentina south of 38° S, such as *Liolaemus tenuis, L. lemniscatus, L. pictus,* and *L. cyanogaster*.

Various bioclimatic classifications have been proposed for Chile, although in general they all describe categories of a latitudinal climatic gradient (e.g., Kuschel 1960). For example, Di Castri (1968) subdivided the zones of moderate altitude of the geographic range where most of the species of this chapter are distributed into a series of ecoregions of increasing humidity and cold toward the south (Fig. 10.2a, b), a pattern generated in part by the prevailing winds that bring moisture from the Pacific Ocean. This area ranges from the arid Mediterranean to the north (with a southern limit near 33° S), passing through the subhumid (34° S to 36° S), to the Oceanic which starts from 39° S southward in Araucanía. At this last latitude, there is a marked break in the climatic conditions, which is the limit between the mesomorphic zone (mainly Mediterranean) and the hydromorphic forested, humid, and cold zone. To the East, and throughout all the previous zones, the high Andean ecoregion is located.

### *10.2.2 Past Climate Changes and Predicted Phylogeographic Patterns*

Southern South America has been exposed to recurrent climatic changes in the past (Heusser 2003), which caused important changes in the geographic distribution of the biota (Turchetto-Zolet et al. 2012; Ruzzante et al. 2008). In this part of the Earth, glaciations occurred since the end of the Miocene, approximately 6 Ma, with an accentuated effect on the Andean relief during the Pleistocene, for about 1 million years, with the Great Patagonian Glaciation (Rabassa et al. 2011). Associating the glacial dynamics with the relief and latitude in Chile, the effects of past climate changes were of greater intensity in the mountainous heights and of greater extension toward the south, where they affected lower areas too (Fig. 10.3a, b).

According to this, it is reasonable to predict the detection of signals of greater demographic and distributional changes at higher latitudes. Although phylogeographic processes should be understood as accumulated phenomena along multiple glaciations (Klicka and Zink 1997), the most cited event is the most recent, the Last Glacial Maximum (LGM). This occurred approximately 23,000–18,000 years ago (Hulton et al. 2002) and modified the landscapes throughout the entire temperate forest distribution of the Southern Andes due to the presence of an ice shield that extended from 36° S to 56° S. Although marginally, it extended northward between 38° S and 34° S, following the heights of the Andes mountain range (Hollin and Schilling 1981; Heusser 2003). During LGM, the sea level dropped by 130 m (Fig. 10.3c), connecting the islands near the coast with the mainland. This would have allowed some species to temporarily colonize habitats that subsequently

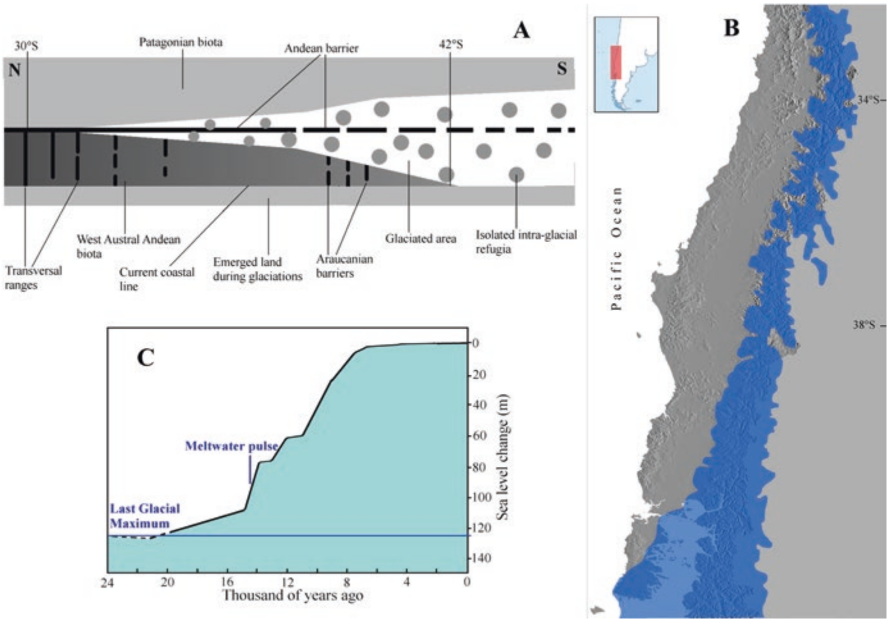

**Fig. 10.3** (**a**) Generalized model for south-central Chile, showing geographic and paleoclimatic attributes of phylogeographic importance. (**b**) Last Glacial Maximum (LGM) extension in central-southern Chile. (**c**) Variation of the sea level from the LGM to the present (based on Fleming et al. 1998)

disappeared again during the interglacial phases. During each glacial event, the forest and its associated fauna would have been displaced from their higher ranges and expanded to the north and to lower altitudes (e.g., *Austrocedrus chilensis*; Souto et al. 2015), caused by higher humidity and lower temperatures (Villagrán et al. 1995). The glaciers probably reached sea level south of the Piuchén Mountain Range on the island of Chiloé (approx. 42° S), thus extending to the southern tip of South America (Fig. 10.3b, Chap. 4). Although relatively continuous, this glacial shield would have sheltered small ice-free refugia, inserted onto an icy matrix, in small Andean valleys and active volcanic zones. In these "ice-free islands," there would have persisted populations that later functioned as sources of recolonization, once the ice retreated. For example, both the Ñuble's Andean zone (37° S) and the Lonquimay Valley (38° S), in Chile, probably remained free of ice (Vera-Escalona et al. 2012). The occurrence of intraglacial refugia (probably many were cryptic refugia) could explain the current patterns of genetic variation in some organisms such as trees, lizards, freshwater crabs, and amphibians, among others (Xu et al. 2009; Nuñez et al. 2011). In a phylogeographic review, Sérsic et al. (2011) proposed hypotheses on refugia and probable routes of dispersion, both for Patagonia and for the Chilean slope. For example, and mainly for plants, they proposed the existence of refugia near the Pacific coast, including the Cordillera de la Costa, north of 42° S. In summary, the phylogeographic consequences of the glacial phases on the biota of the western slope of the Southern Andes seem to include (1) fragmentation and reduction of effective population sizes during the presence of ice shields, with a gradually greater effect toward greater latitudes, and (2) expansions subsequent to the glaciations, also with stronger signals at higher latitudes. An opposite pattern should be evidenced for the less affected populations of Central Chile, mainly along the Pacific coast. These areas would have been relatively stable (Villagrán 1991; Villagrán et al. 1995; Markgraf et al. 1995), for which we should expect clearer signs of historical demographic equilibrium.

## 10.3 Genetic Patterns and Phylogeographic Processes in Chilean Lizards

According to the underrepresentation of South American phylogeographic studies in comparison to what has been done for the Northern Hemisphere, the lizards of Chile have been seldom studied in this regard (Turchetto-Zolet et al. 2012). Even adding the phylogeographies of the other Chilean herpetozoa, such studies are scarce. For example, for snakes there is only one work in *Philodryas chamissonis* (Sallaberry-Pincheira et al. 2011), and for amphibians a few others (e.g., Vásquez et al. 2013; Victoriano et al. 2015).

For Chilean lizards, such works have mainly considered species of the genus *Liolaemus*, especially for those species distributed in the center-south areas of the country. Although restricted to this latitudinal range, these species have the virtue of covering a varied range of geographical scenarios (Fig. 10.4). For the other ten genera present in Chile (Vidal and Díaz-Páez 2012), there are only a couple of works on *Microlophus* species, predominantly distributed in coastal environments of the northern desert.

### *10.3.1 Intraspecific Evolution of Chilean* Liolaemus

*Liolaemus* is the genus with the greatest number of species in the south of South America, and for which a high rate of new species descriptions continues, suggesting that its real diversity is still far from being well known (Abdala and Quinteros 2014; Avila 2010; Chap. 9). The recent description of several species of the genus on the western slope suggests that this trend will continue (Esquerré et al. 2013; Troncoso-Palacios et al. 2015, 2016, 2018). Similarly, a considerable number of species have been described on the Argentinean side, including cryptic diversity (e.g., Abdala et al. 2015; Avila et al. 2004; Medina et al. 2014; Morando et al. 2003; Olave et al. 2017). With more than 250 species, this genus is distributed from the central coast of Peru to the south, through Bolivia, Paraguay, Chile, and Argentina, reaching southward to Tierra del Fuego. At the East, it reaches the Atlantic coast of

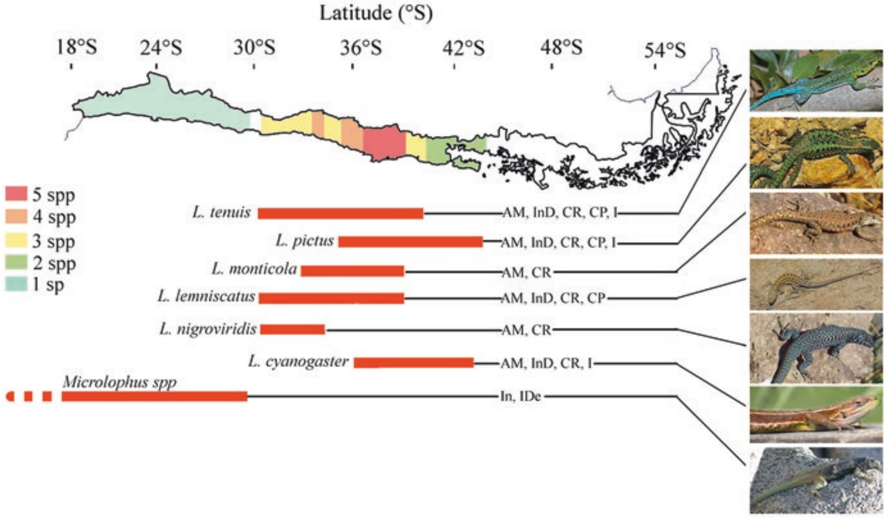

**Fig. 10.4** Summary graph detailing the species or species groups analyzed in phylogeographic studies in Chile. The horizontal bars represent the latitudinal distribution. Presence in different physiographic units are indicated by acronyms: *AM* Andean mountain, *InD* Intermediate Depression, *IDe* Inner desert, *CR* Coastal Range, *CP* Coastal plains, *In* intertidal, *I* islands. Color scale corresponds to the number of studied species according to latitude in the map. Photo credits: *L. cyanogaster* (Jorge Álava), *L. monticola* and *L. nigroviridis* (Carlos Garín)

Uruguay and the southeast of Brazil (Etheridge and Espinoza 2000). Its great taxonomic diversity and wide geographic distribution, through topographically and climatically diverse landscapes, is accompanied by a remarkable ecological versatility. Some species inhabit rocky or sandy environments, others are present in wooded or scrubland environments, and others are typical of open steppes such as Patagonia (Díaz-Gómez and Lobo 2006). In some widely distributed species, as is the case of some in central-southern Chile, their populations occupy very contrasting environments and gradients (e.g., arid Mediterranean to humid Oceanic). Their evident tendency to diversification, adaptation to diverse environments, moderate vagility, and condition of ectothermic organisms especially sensitive to physical environmental conditions make these lizards good models for phylogeographic studies (see Camargo et al. 2010; Wollenberg et al. 2019).

*Liolaemus* seems to have had an Andean-Patagonian origin (Díaz-Gómez and Lobo 2006; Vidal and Díaz-Páez 2012). Among the visionary classic herpetologists, Hellmich (1951) had already suggested that the current diversity and distribution would be a consequence of expansions and contractions of older distributions, associated with the glacial and interglacial processes during the Tertiary. The Andes as a promoter of basal divergences in *Liolaemus* is already present in the proposal of Laurent (1983), who subdivided it into two subgenera, according to the distribution of this great geographical barrier: one corresponding to *Eulaemus* or the species present on the Argentine side and the other to *Liolaemus* or western group. However, the diversification of these two groups should not be oversimplified by association with a single vicariant event generated by the Andes. For example, molecular evidence suggests that the origin of viviparity in *Liolaemus* would have occurred several times mediated by a complex of vicariant and dispersion events, some even prior to the definitive uplift of the Andes (Schulte et al. 2000; Schulte and Moreno-Roark 2010). This intricate process of diversification could explain the occurrence in the south of a *Liolaemus* distribution that does not "respect" the Andean vicariance, erasing the reciprocal monophyly between the two sides of the mountain range. Recent estimates based on the molecular clock for the *Eulaemus* group suggest that the beginning of the diversification of this clade would have occurred approximately 19 Ma, and several of the divergences between sister species would be about 5 million years (Fontanella et al. 2012). According to preliminary estimates for pairs of Chilean species, the divergence of *L. lemniscatus*-*L. tenuis* would have occurred approximately 3.7 Ma (Vera-Escalona, unpublished data). The genetic diversity of some Chilean species would be about 2 million years old (Muñoz-Mendoza et al. 2017; Vera-Escalona et al. 2012). This indicates that the phylogeographic processes to which the *Liolaemus* species have been exposed would have covered a large part of the Pleistocene climate changes on an extremely heterogeneous geographical scenario. Phylogeographic studies tend to mainly consider recent glacial events, such as LGM as a causal factor of diversification, probably because traces in the genome are also more evident for younger processes (Late Pleistocene Origins model, LPO). However, such consequences should be interpreted in light of the summed effects of several older glacial processes (Klicka and Zink 1997). The evidence gathered so far for the Chilean *Liolaemus* suggests trends largely consistent with the physical and paleoclimatic attributes of the western slope of the Southern Andes. Their patterns are characterized by high levels of genetic diversity, with an accentuated structure, often detectable in small geographic ranges, and with evidence of contrasting demographic processes according to latitude and altitude. In some cases, the magnitude of the divergences also suggests the existence of cryptic diversity, probably cases of species that have not yet been delimited.

### *10.3.2 Lizards Evolving Within Mountains*

An interesting case of *Liolaemus* species that have evolved in close association with mountainous ecosystems is the *monticola* group. These saxicolous species characterized by a dark coloration, probably as a result of adaptations to Andean basaltic environments, are found above 1000 m, between 30° S and 40° S. In the case of the species *L. monticola*, some of its populations at the latitude of Santiago (approx. 33° S) are connected to the Coastal Range due to the existence of transverse ranges at that latitude, where the elevated terrain would have worked as corridors. Because of its distribution, this species complex probably diversified under the effects of extreme relief conditions and, due to its altitude, probably under important effects of glaciations and volcanism. In fact, some of its species are closely associated with volcanic systems, such as *L. chillanensis* and *L. villarricensis*. During times of allozyme and karyotype methodology, the first works with some phylogeographic hypotheses for this group were already emerging in the 80s and 90s. More recently, Lamborot et al. (2003, 2012) found interesting patterns of differentiation of chromosomal races in *L. monticola*, associated with Andean fluvial barriers (Aconcagua and Maipo Rivers in Central Chile, approx. 33° S), with low rates of introgression. Some of these studies revealed an interesting geographic variation at the chromosomal level, in some cases with morphological agreement and with considerable levels of evolutionary divergence (Lamborot 1993, 1998; Lamborot et al. 1981; Lamborot and Alvarez-Sarret 1993; Lamborot and Eaton 1992, 1997; Lamborot and Vásquez 1998). For example, Lamborot et al. (1981) found differences in the fundamental number of chromosomes between the previously considered subspecies of *L. monticola* (*L. m. monticola, L. m. chillanensis,* and *L. m. villarricensis*), allowing to distinguish between the nominal subspecies and the other two distributed in the south. Genetic variability based on allozymes for two syntopic morphs from the Chillán volcano (*chillanensis* and *Liolaemus* sp.) evidenced absence of gene flow between both, which also differ in an attribute of high constancy in the genus as is the presence of precloacal pores in males. This served as motivation to suggest they represented two co-distributed cryptic species (Torres-Pérez et al. 2003). Integrating genetic and morphological evidence, the hypothesis that the subspecies involved cryptic diversity at the level of different species was strengthened. It was also established that these do not conform a natural group but polyphyletic (Torres-Pérez et al. 2009, 2017). This suggests evolutionary processes that led such unrelated species to converge similar phenotypic traits, probably conditioned by common environments. For these species, one of the components that has generated geographic discontinuity in the Andes has been the presence of rivers that could have functioned as barriers for a long time and have promoted differentiation (Lamborot and Eaton 1992). Vásquez et al. (2007) added alloenzymatic evidence that reinforced the idea that morphological and genetic differentiation in *L. monticola* was mediated by the action of fluvial systems, and Torres-Péres et al. (2007) suggest that the action of fluvial barriers for this group of *Liolaemus* would have been key in its diversification over a prolonged time. Other groups of mountain lizards of Chile could fit into this model and have not yet been analyzed in a phylogeographic context, as is the case of several species of *Phymaturus* distributed in the intricate Andes between 25° S and 45° S. Seven of the nine species have been described for Chile during the 2000s, and several of them after 2010 (Núñez et al. 2010; Pincheira-Donoso 2004; Troncoso-Palacios and Lobo 2012). A comprehensive recent study has revealed for this genus the existence of great diversity not previously described (Morando et al. 2013) and, although widely distributed in Patagonia, several of its species would have been generated in intra-Andean scenarios. Another case of lizards that would have evolved in montane environments is that of *L. nigroviridis*, a saxicolous species from Central Chile (30° S to 34° S). Although three subspecies were proposed

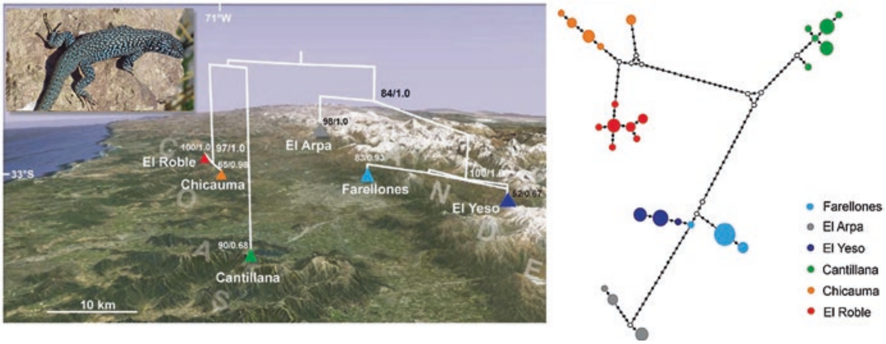

**Fig. 10.5** Phylogenetic tree and haplotype network of the Andean species *Liolaemus nigroviridis* (adapted from Cianferoni et al. 2013. Photo of *L. nigroviridis* by Carlos Garín)

for this species in the 30s to 60s based on their allopatric distribution and putative morphological differences, these were not later evidenced by morphological and karyotypic analyses, leaving *L. nigroviridis* as monotypic (Núñez and Jaksic 1992; Valencia et al. 1979). A recent phylogeographic study based on mitochondrial DNA showed an important evolutionary divergence between populations of Andean habitats and those of the Coastal Range, at the same latitude (Fig. 10.5), which would have occurred approximately 2.7 Ma (Cianferoni et al. 2013).

The interesting thing about their diversification processes is that they would have occurred according to a dynamic of isolated high-altitude environments ("Sky Islands"), where the valleys would have functioned as barriers most of the time. The permeability of such valley barriers probably varied according to the glacial cycles (greater connectivity for this species in low areas during each glaciation), allowing at those stages the exchange between coastal and Andean populations. However, this explanation should be reconsidered after taking into account mtDNA information from a dense geographic sampling. A molecular study that included other species of the genus, revealed *L. nigroviridis* could be polyphyletic (Torres-Pérez et al. 2017). In summary, lizards restricted to high altitude in the Andes are a good model for the study of phylogeographic diversification and speciation in montane environments, which may have been due to prolonged processes of isolation and environmental instability. It also seems frequent that in these scenarios species would have originated in restricted geographical areas within an extremely discontinuous landscape. The great degree of geodiversity of the Andes, its numerous rivers, and the complex spatial distribution of the glacial effects had to play an important role in the processes of diversification of lizards. In this sense, the Andes has not only generated strong vicariant effects resulting in the Eastern Patagonian lizards and the Chilean group in the Pacific slope, but it has been a prolific scenario of in situ diversification, functioning as a true "species pump" (Sedano and Burns 2010).

### *10.3.3 Diversification Throughout Gradients, Barriers, and Glaciations*

Long-standing gradient scenarios offer certain advantages in evolutionary studies because, by generating different selection pressures and gradual magnitudes of gene drift, they can, for example, promote parapatric diversification (Losos 2009). Environmental gradients have been highlighted as modulators of species richness and with complex synergies between topography, climate, and vegetation (Moura 2016). Few species of lizards offer the advantage of a wide distribution west of the Andes, as is the case of *L. tenuis*. This makes it a good model to understand how environmental forces have acted in processes of intraspecific diversification, along what could be called a good natural experiment. This lizard has evolved in a scenario that covers more than 1000 km from North to South, exposed to very diverse biogeographic and paleoclimatic historical conditions. It has arboreal tendencies, and it is oviparous. It is distributed in Chile from the Coquimbo Region in the north (Mediterranean shrublands landscapes, ca. 30° S) to the humid forested area of the Los Ríos Region (approx. 41° S), with some peripheral populations on the eastern slope of the Andes, in the Province of Neuquén, Argentina. Altitudinally, it extends from sea level on the Pacific coast to the Andean foothills. Although some populations can reach 1800 m.a.s.l., in most cases, it does not exceed 1000 m. This lizard has a remarkable ecological versatility, and it is abundant both in arboreal vegetation and scrubland, as well as in urbanized environments (Pincheira-Donoso and Núñez 2005). Adults show an evident sexual dichromatism. The male is of an extremely striking color, which makes it easily distinguishable, with yellow, green, and blue spots (Fig. 10.6). Two subspecies have been argued fundamentally for their patterns of dorsal coloration (Müller and Hellmich 1933): *Liolaemus t. tenuis*, from the Mediterranean environments of Santiago, approx. 33° S, and *L. t. punctatisimus* with type locality on the coast of the transition climatic zone in the Biobío Region (Lota, approx. 37° S). However, these lizards show a rather clinal variation, where the green tones increase toward the south, which does not ratify both subspecies from this point of view (Vidal et al. 2007). A geometric morphometrics study showed that populations from the humid range in the south differ slightly in its head shape from the rest of their populations (Vidal et al. 2005). Although, according to the above, *L. tenuis* shows some phenotypic variation, this variability is not distributed with a clear geographical structure. This is a morphologically conservative species considering its wide geographic range. Contrary to what its morphology suggests, *L. tenuis* is genetically a very variable species. This was already suggested by a study of isoenzymes which showed a tendency to group populations according to their latitudinal range (Vidal et al. 2004). The recently published phylogeography for this species shows suggestive arrangements of the important role played by geography and climatic changes of the Pleistocene in south-central Chile (Muñoz-Mendoza et al. 2017). This study covered the entire distribution of the species with a dense sampling (84 localities) and was based on mitochondrial and nuclear genes, plus five microsatellites. The geographical distribution of their lineages suggests

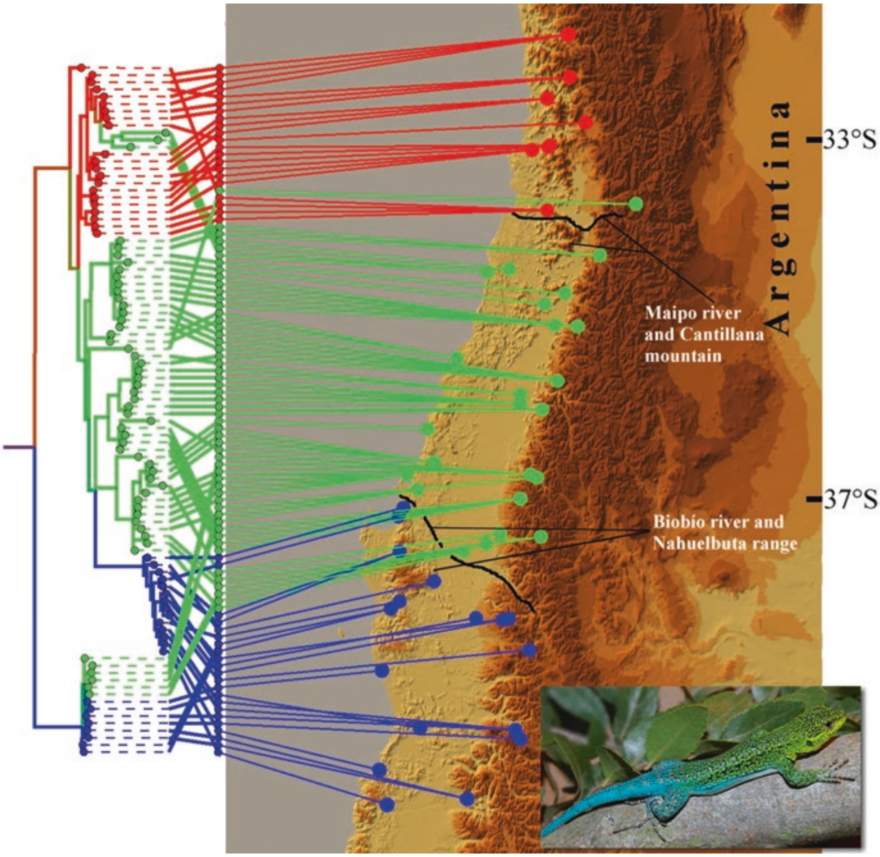

**Fig. 10.6** Lineages distribution of *L. tenuis* and its association with the main river-mountains barriers in Central-southern Chile

important phylogeographic breaks associated with some Chilean rivers and mountains, among which the Maipo River (approx. 34° S) and the Biobío River (approx. 37 °–38° S) stand out (Fig. 10.6). Both fluvial systems have previously been hypothesized as probable barriers for other species. An additional interesting pattern in *L. tenuis* is its high number of lineages, several with deep divergences, and geographically structured, predominantly in the central-northern area of its distribution. The mitochondrial genetic diversity of the species would have an approximate age of 1.8 million years, when its two main lineages would have diverged. The first clade has a wide geographic distribution that covers almost the entire range of the species and whose diversity would have originated approximately 1.3 Ma. The second clade is typical of the wet zone, south of 37° S, and it is sympatric with the southern part of the previous clade (Fig. 10.6). This southern clade corresponds to a much more recent lineage (ca. 200,000 years), and its distribution coincides with an area where the ice sheet of the LGM acquired greater continuity (Rabassa et al. 2011).

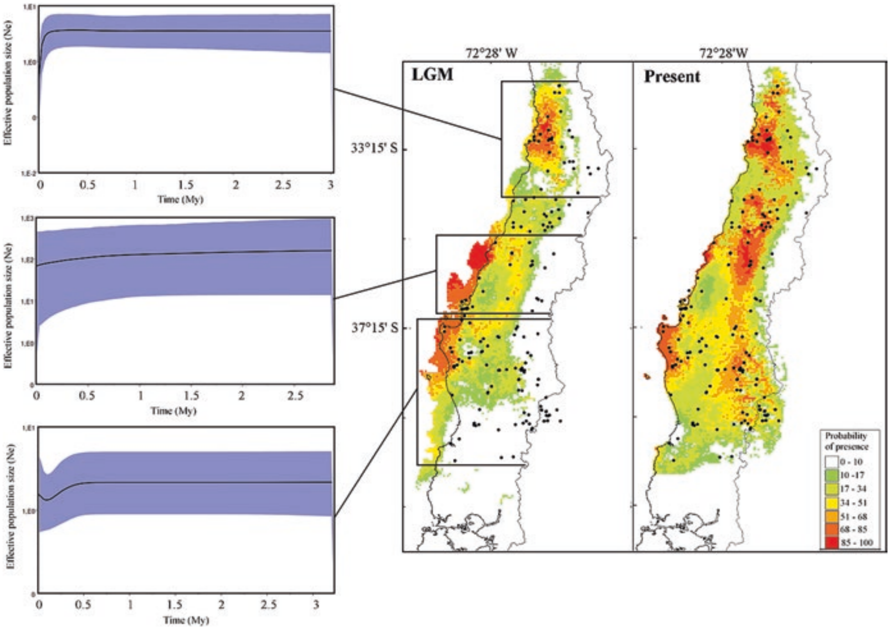

**Fig. 10.7** Estimates of the historical variation of the effective population size (Ne) for the three main clades of the lizard *L. tenuis* (left) and ENM maps for the species (right) (adapted from Muñoz-Mendoza et al. 2017)

In contrast to the central-northern populations, there are interesting signs of recent recolonizations in the species austral range and, apparently, their historical demographic behavior has included considerable reductions in their effective population sizes, suggested by both analysis of Bayesian Skyline Plot and by past and present habitat suitability modeling (Fig. 10.7) (Muñoz-Mendoza et al. 2017). This is an interesting phylogeographic pattern that is consistent with the paleoclimatic history and geographic attributes of central-southern Chile, as narrated in a previous section of this chapter. The most stable areas for this species tend to be distributed at low altitudes, north of the Biobío River and near the Pacific coast (Fig. 10.7). According to the environmental history from south of Araucanía (approx. 38° S), where the two main lineages of *L. tenuis* are co-distributed, this species has experienced recent recolonizations from refugia, with range expansions, which resulted in a large secondary contact zone. The estimated patterns of historical gene flow are concordant with the above, where not only coastal populations would have functioned as a source in the south, but relict populations within the ice limit in the Andes would have recolonized from east to west. The geographical boundary concordant with the oldest divergence within *tenuis*, close to the Biobío River and to the northern edge of the Nahuelbuta mountain range, seems to have functioned as a complex of barriers in interplay with a climatic transition zone.

Apparently, this could be a good scenario to address not only phylogeographic questions but from a geogenomic and phylogeological point of view (Acosta et al. 2014; Baker et al. 2014; Fritz and Baker 2017). At this latitude, in addition to the Nahuelbuta range, part of the Coastal Range extends inland, approaching the Andes and narrowing the valley. Also, in this area there is a series of at least three deep fluvial canyons that cross the Intermediate Depression (e.g., Collipulli), which, in the past, during phases of rainiest times and melting (e.g., during meltwater pulses, after the LGM, from 15,000 to 8000 years ago; Fig. 10.3c; Fleming et al. 1998), could form a set of barriers. If a greater effect of the glaciations from this latitude to the south is added, the sum of all these factors could explain the phylogeographic discontinuity in this part of the *L. tenuis* distribution. For this area, reduced range of habitat and decreases in effective population sizes in Araucanía during LGM have also been detected in the lizard *L. lemniscatus* (Coronado et al. unpublished data). In addition, the distribution of intraspecific lineages coinciding with this latitude largely agrees with the delimitation of Chilean biogeographic units distinct to the south and north of such limit (e.g., Artigas 1975; Pisano 1954). This is indicative of environmental processes that have affected the intraspecific scale and would also have generated evolutionary effects at community level (species composition). For genetic and species diversity effects of environmental stability, there is published evidence for lizard assemblages from other parts of the world (Araújo et al. 2008; Werneck et al. 2012).

### 10.3.4 A Complex History in Forests and Islands

If we move to more humid and cold wooded environments of Chile, where lizard species decline in their richness, we find a very interesting history of refuges, vicariances, and dispersions. *Liolaemus pictus* is a species adapted to temperate forests dominated by *Nothofagus* and also inhabits *Araucaria araucana* formations. This lizard is distributed from sea level to 1600 m and in Chile it ranges from the Andes of the Maule Region (approx. 35° S in Alto Huemul Sanctuary; Ramírez-Álvarez and Troncoso-Palacios 2016), to the region of Los Lagos (approx. 43° S) (Vera-Escalona et al. 2010). In its southern distribution, this species inhabits both continental environments and the islands of the Chiloé archipelago. It is also present in the Province of Neuquén, Argentina, on the eastern slopes of the Andes, in forest environments that communicate with Chile through trans-Cordillera valleys. Approximately 50% of the area of its current distribution would have been covered by ice at the LGM. Both the geographical distribution and the moderate vagility of *L. pictus* suggest that it had to endure important evolutionary consequences due to the glaciations. This lizard shows an accentuated variation of coloration, which has motivated the description of six subspecies. Although one of them is already addressed in the literature as a distinct species (*L. septentrionalis*; Ramírez-Álvarez and Troncoso-Palacios 2016), given its evolutionary closeness and lack of a formal description, for purposes of phylogeographic analysis, it is treated in this chapter as part of *L. pictus*. The adaptations of these lizards that enable them to inhabit colder environments in comparison to other *Liolaemus* include its viviparous reproduction, and studies on its thermal ecology indicated it as a species with plasticity and low thermal requirements, even depending on which clade is involved (Artacho et al. 2017). Evidence suggests that populations of higher elevation environments show lower activity temperatures than those of low environments (Gutiérrez et al. 2010; Labra 2015), suggestive of adaptive variations according to the climate regimes to which different populations have been exposed. Little is known about their behavior and ways of communication. Labra (2015) indicates that, as it is true in general for *Liolaemus*, its displays are relatively simple in comparison to other groups of lizards. *Liolaemus pictus* is often observed in syntopy with *L. tenuis*, in relatively open wooded habitats, against which it tends to behave aggressively, imposing its larger size. Its isolation in several islands of the Chiloé archipelago seems to have generated interesting morphological and physiological differentiations (Vidal and Sabat 2010). According to comparisons using geometric morphometrics, this species shows significant differences in the cephalic shape (e.g., size of the eye orbits), which has been explained by allusions to adaptations to a differential use of resources between islands and the continent (Vidal et al. 2006). *Liolaemus pictus* is a relatively young species. An estimate based on the mitochondrial gene Cyt-b indicates that the age of the most recent common ancestor is 750,000 years (Vera-Escalona et al. 2012), which is notoriously lower than other *Liolaemus* species (see Olave et al. 2017). Another divergence age estimate based on the same gene suggests divergence between the populations of the Isla Grande de Chiloé and its neighboring islands in no more than 860,000 years (Vidal et al. 2012a, b). The woody landscapes in southern Chile generally appear to be composed of communities and taxa younger than the Mediterranean biota, based both on their vegetational composition and on assemblages of invertebrates (Markgraf and McGlone 2005; Segovia et al. 2013; Whitlock et al. 2001). This has been interpreted as a consequence of a fluctuating paleoclimatic history, which could also have influenced the origin and diversification of *L. pictus*.

The oldest divergence for the two main clades within *L. pictus* would have occurred during the second half of the Pleistocene, whose geographical limit, like *L. tenuis*, coincides with the north of the Araucanía at the latitude of Malleco, an area for which the probable role of a complex of old barriers was previously discussed in this chapter. The first of two main clades (North clade) extends from the north of the Araucanía at the Llaima Volcano (38° 41′ S) to the Maule Region, the northernmost limit of the species (approx. 35° S), in the *Nothofagus* forests that extend to the north progressively more discontinuously along the Andes. In this lineage are also included the populations of the Nahuelbuta coastal massif. Although, after the work of Vera-Escalona et al. (2012), all this northern lineage was suggested for *septentrionalis*, it is interesting the existence of considerable divergences within this clade, which perhaps should be reevaluated against the eventual existence of more than one taxon. At least three well-differentiated clades with allopatric distribution are distinguished in this northern group: one for Nahuelbuta, another for the Andean from the Llaima Volcano in the Malleco National Reserve, and a third for

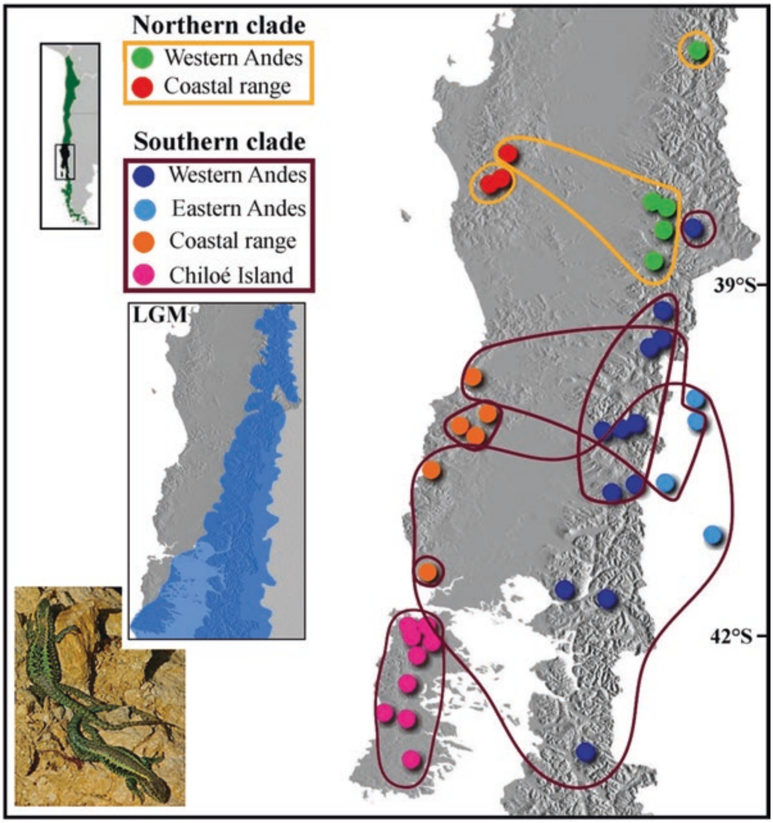

**Fig. 10.8** Geographic distribution of the mitochondrial clades of the lizard *L. pictus*. The extension of the ice during the LGM is also shown

the valley of Las Trancas in Ñuble (Fig. 10.8). The notorious differentiation between these populations could well have been due to the cyclical range expansions of the forests whose distribution changed during the glaciations, expanding to the north during colder and wetter periods (Villagrán 2001); after their retreat to the south, during interglacial phases, left fragmented populations that would have promoted evolutionary divergence. Being part of one of the distributional extremes of the species, this pattern could be explained by the "central marginal hypothesis," which proposes that peripheral populations tend to be associated with greater and more frequent events of demographic instability, smaller effective population sizes, and with greater genetic differentiation (Eckert et al. 2008). The second main clade of *pictus* (austral lineage) covers a much more extensive territory (Fig. 10.8), from the north of Araucanía (approx. 39° S) to insular and mainland Chiloé in the south (ca. 44° S). Three interesting aspects of the history of *L. pictus* can be read in the topology of this great southern lineage, which is evidenced by estimates of gene flow, structuring patterns, historical population sizes, and inferred historical geographic distribution. The notorious absence of reciprocal monophyly between populations from the Andes and from the Coastal Range, where even populations in the Argentine side are closely related to the coastal populations of Chile, is suggestive of a complex historical connection between the populations of both mountain ranges. Important magnitudes of bidirectional historic East-West gene flow, coupled with an increase in habitat suitability in the valleys of the Intermediate Depression during the LGM, suggest that these populations were able to recurrently connect. A dynamics of descent into the valleys during the glaciations and subsequent recolonization of mountain ranges during interglacial periods has been hypothesized for trees in this area, such as for *Austrocedrus chilensis* (Souto et al. 2015; Pastorino and Gallo 2002) and *Araucaria araucana* (Ruiz et al. 2007), both species that are part of the *pictus* habitat. Greater historical connectivity compared to the demographic behavior of the northern populations, and compatible with range expansions in the south of the *L. pictus* distribution is suggested by a latitudinal gradient of differentiation according to a genetic landscape analysis, with less structuring toward the south (Fig. 10.9). This is consistent with estimates of a greater historical reduction in effective population size during the LGM in the southern lineage (based on Bayesian Skyline Plots). A second interesting aspect is that apparently *L. pictus* would have persisted in numerous intraglacial refugia (cryptorefugia and/or microrefugia), from which it would have expanded its range during the interglacial phases. As in *L. tenuis*, although in *pictus* it would have been much more evident and extensive, such refugia would have worked as sources that contributed genetic variability to lower areas, and even to those of the Coastal Range. As previously indicated, the evidence of glacial refugia has been indicated for different taxonomic groups, such as for the rodent *Abrothrix manni* (Valdez and D'Elía 2018), trees (Allnut et al. 1999; Arana et al. 2010; Bekessy et al. 2002; Pastorino and Gallo 2002; Marchelli and Gallo 2006), freshwater fishes (Cussac et al. 2004), amphibians (Nuñez et al. 2011), and crustaceans (Xu et al. 2009). The recolonization of *L. pictus* from different continental refugia was also suggested by Vidal et al. (2012a, b) in a beautiful phylogeographic reconstruction for the austral range of the species. A third emergent attribute in the spatial arrangement of lineages of *L. pictus* is the lack of molecular evidence to support the existence of most of their subspecies previously based on morphology, although with two clear exceptions associated with their distributional extremes. One of them was already highlighted, which is the case of northern *septentrionalis*, and the other is the case of southern *chiloensis* subspecies, on the Isla Grande de Chiloé (approx. 42° S–44° S). Although it is not a complete reciprocal monophyly, most of the genetic diversity of the Isla Grande de Chiloé is exclusive for this island and forms a clade of considerable divergence. Although during each glaciation the sea descended, being able to connect islands with the continent at that latitude (Pirazzoli 1991), apparently the phylogeographic signals (and not only for *L. pictus*), do not clearly shows that. Even for larger species such as the Andean southern deer *Pudu pudu*, a large molecular divergence was detected for this species between the population of the island and the continent (Fuentes-Hurtado et al. 2011).

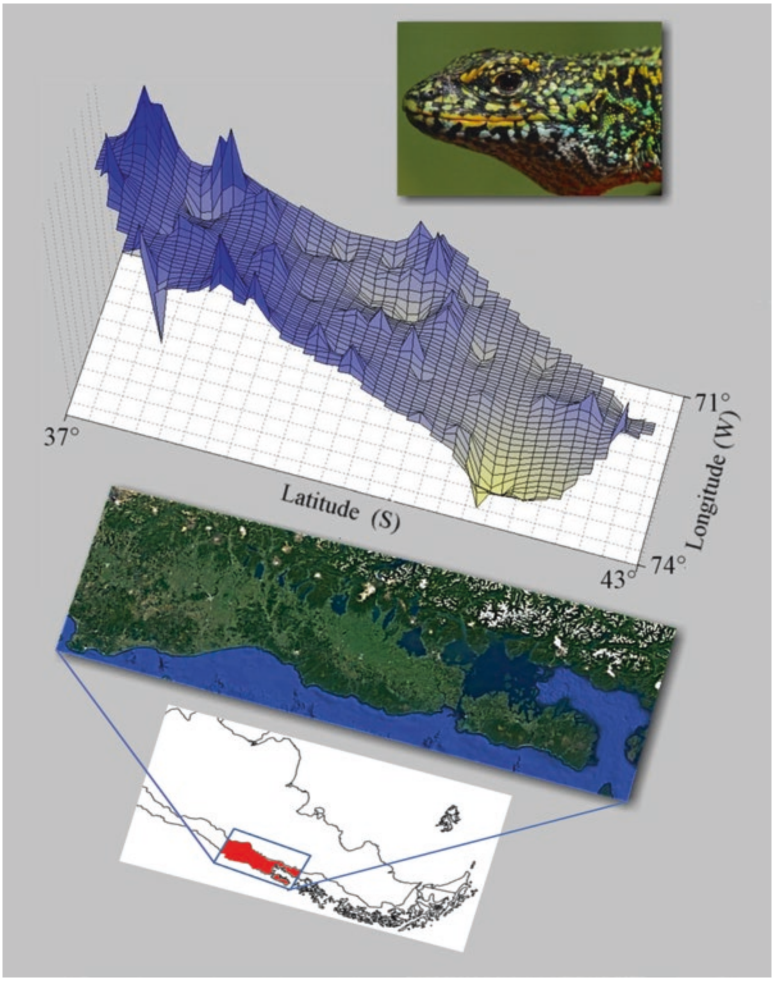

**Fig. 10.9** Genetic landscape shape interpolation analysis for the distribution of *Liolaemus pictus* based on mtDNA. Blue and high areas in the graph correspond to higher levels of genetic structuring. Low and yellowish areas correspond to low genetic structure

Given that the sea descended repeatedly, establishing island-continent bridges, a vertebrate of that body size should show fewer structuring signals. Vidal et al. (2012a, b) also detected strong structuring for *L. pictus* between the Chiloé Island and the mainland, dating it as a divergence predating the LGM. Although such an evolutionary divorce is indicated as previous to the last glaciation (ca. 860,000), the marked evolutionary differentiation of these populations was explained by a probable recent configuration of the shallow continental shelf. If so, this scenario would not have provided the conditions to form land bridges for a sufficient time to generate island-continent exchanges in *L. pictus*. However, in relation to the age of this species, the Chiloé-continent disconnections encompass most of the evolutionary history of this lizard. A complementary explanation for this great structuring is that either no continuous terrestrial connection was established with the continent, or if it happened, the emerged shelf did not come to form a continuous ecosystem compatible with species highly dependent of a dense forest ecosystem. Evidence based on microsatellites and mtDNA in the small felid *Leopardus guigna* suggests that this cat has had greater connectivity between the Island of Chiloé and the continent (Napolitano et al. 2014). This is a species that, although it is an inhabitant of the forest, is a more generalist in habitat use than *L. pictus*, being able to be detected in more open environments, such as scrub and savanna (Iriarte et al. 2013). The dynamics of colonization of the other small islands of the Chiloé archipelago by *L. pictus* has been somewhat different, where there would have been greater levels of connectivity, both with the mainland and with the Isla Grande de Chiloé. Vidal et al. (2012a, b) explained such minor structuring, alluding that terrestrial connections were more likely, where the genetic composition of such islands suggests a complex history of young colonization routes (even after the LGM), both from the mainland and from Isla Grande de Chiloé. In summary, the phylogeography of *L. pictus* is a good example in which the diversification within a lizard species has gathered different patterns and processes depending on its geographic range. In the north of its distribution, it would have been affected by the distributional dynamics of the forests (expansion-contraction), due to past climatic changes. In its central range, an Andean-Coastal exchange dynamic is highlighted, including intraglacial refugia, and in the insular southern range populations, the changes in sea level, the presence of extensive glaciers, and their thaws would have formed a complex history of barriers and land bridges.

### *10.3.5 Comparative Phylogeography: Shared Histories in Co-distributed Lizards*

Comparative phylogeography (CP) aims to investigate the eventual spatial and temporal agreement of divergence processes and demographic histories of two or more co-distributed species (Gutiérrez-García and Vázquez-Domínguez 2011). In this sense, CP has much to contribute to historical biogeography by gathering evidence of processes that could explain the concordances in spatial distribution of genetic diversity at the community level (Arbogast and Kenagy 2001; Zink 2002). For example, it can identify suites of species that have had a common vicariant history (Moritz and Faith 1998). CP could also be complemented with comparative studies of the phylogenies of community structure, establishing in this way a link between the community ecology and biogeography (Vamosi et al. 2009). Another contribution of CP is that, through its multispecies approaches in common scenarios, it takes advantage of natural experiments, where replicates of species (independent evolutionary units that provide genetic response variables) are useful to infer generalizable processes that can be tested statistically (Bermingham and Moritz 1998). Since its inception, when CP simply consisted of visually contrasting the topologies of different co-distributed species, it has progressed to include sophisticated methods that statistically evaluate hypotheses about common evolutionary histories. The first statistical evaluation estimated the significance of congruent areas-topologies and the construction of supertrees to delimit geographical areas with common evolutionary histories for the species they harbor (Lapointe and Rissler 2005). With the emergence of statistical phylogeography (Knowles and Maddison 2002; Knowles 2004), which considered the use of summary statistics in the frame of coalescent stochasticity, the evaluation of hypotheses of simultaneous and co-distributed vicariances for different species was strengthened (Hickerson et al. 2006). A good example of this approach is the study by Carnaval et al. (2009), which provided evidence for codivergences between amphibian species of the Atlantic coast of Brazil. The incorporation of nongenetic evidence, such as ecological niche models (ENM), has allowed us to evaluate if the historical distribution of populations of different co-distributed species is correlated. If it is a positive result, and if it is consistent with the distribution of lineages of several species, we have evidence that environmental history has influenced co-diversification processes between species (Carstens and Richards 2007; Knowles et al. 2007). CP studies in Chile are still very scarce, and it represents a potentially fertile ground to understand the processes that have affected lizard assemblages as a whole (or for lizards and other kinds of organisms). Although an interesting number of individual studies for plants and animals from Chile have already been published (several of them with wide distributions and co-distributed), the comparative approaches do not exceed four cases.

According to a compilation of phylogeographies for terrestrial vertebrates and plants, which qualitatively integrates publications of co-distributed species (Sérsic et al. 2011), some congruent patterns suggest that quaternary and pre-quaternary geological events would have promoted the concerted diversification of some taxa in southern South America. Victoriano et al. (2008) found evidence that three species of *Liolaemus* (*L. tenuis, L. lemniscatus,* and *L. pictus*) show significant topological agreement for some of their clades. A supertree based on the integration of the topologies of these three lizard species also showed concordance with the main Chilean bioclimatic zones (mesomorphic, transition, and hydromorphic). These three species showed a significant correlation between the patristic distances of the supertree and the bioclimatic similarity between such areas (Fig. 10.10). As such, we can think that each Chilean bioclimatic zone harbors singular evolutionary histories of their biota, which is interesting both from a biogeographical point of view as well as regarding proposals for conservation areas. This study also suggests that in the Mediterranean area in central Chile, the pair *L. tenuis-L. lemniscatus* could have co-diversified in response to shared vicariant events, which would have been predominant over the effects of glaciations. A study previously commented on in this chapter indicates that important barriers for the divergence of the main clades of *L. tenuis* are due to rivers and mountains (Muñoz-Mendoza et al. 2017).

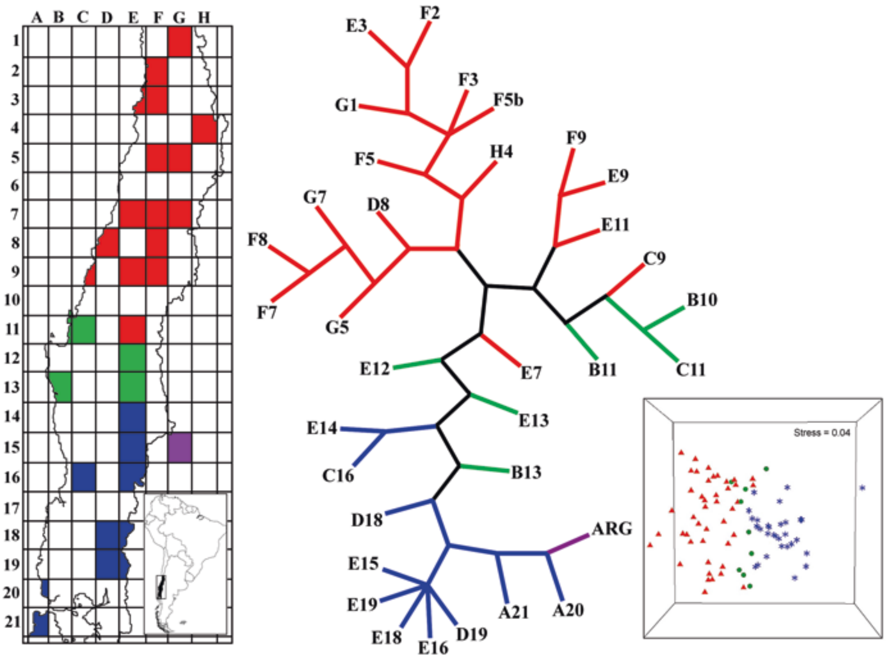

**Fig. 10.10** Supertree of areas based on mitochondrial sequences of the species *L. tenuis, L. lemniscatus,* and *L. pictus*. The acronyms of letters and numbers correspond to the quadrants shown on the map. The colors correspond to general bioclimatic zones of Chile. Red, mesomorphic; green, transitional; blue, hydromorphic or wet zone; violet, Argentinean populations. Below to the left is a multidimensional scaling for localities of the three Chilean zones, based on bioclimatic similarity

The processes that would have affected in a similar and contemporary way these two co-distributed *Liolaemus* could generate not only simultaneous vicariance but also demographic changes in parallel, for example, trends of past changes in their effective population sizes. When associating the values of effective population size of same date estimated by BSP for *tenuis* and *lemniscatus*, a significant positive correlation is observed. This is indicative that past environmental factors generated at the same time result in changes of abundance in both species in similar ways. Further south in the hydromorphic zone, for the species pair *L. tenuis-L pictus*, the glacial cycles would have been those that predominantly structured their shared phylogeographic history, where heterospecific populations could share a history of marked environmental instability promoting concerted diversification. This is corroborated by observing changes in the habitat distribution of both species during the LGM, suggested by niche modeling (Muñoz-Mendoza et al. 2017; Vera-Escalona et al. 2012). For this geographic range there is also phylogeographic evidence for other two species, *L. pictus* and *L. cyanogaster*, with concordant evolutionary responses that occurred during the Middle Pleistocene (Vidal et al. 2012a, b). Within this same area, including the Chiloé archipelago, the complex interaction between the quaternary glacial cycles with geography would have generated concordant phylogeographic patterns between the lizard *L. pictus* and the amphibian *Batrachyla leptopus*. It is really interesting that taxa of contrasting biologies could suffer similar evolutionary consequences (Vidal et al. 2016). Among the common processes for this lizard-anuran pair, there is the apparently simultaneous divergence of populations of Isla Grande de Chiloé with respect to the continent, a complex colonization dynamic of the small islands, and the occurrence of refugia both on the Pacific coast and east of the Andes. CP studies in Chile suggest that this scenario could have generated common evolutionary histories, not only for lizard species but for other components of the community. As previously mentioned, there are phylogeographic studies of several taxa that share a large part of their distribution, including plants, terrestrial vertebrates, and invertebrates, which are available to test hypotheses of concerted evolution at community level. Among the interesting geographical scenarios of the west of the Andes that could be evaluated regarding its diversifying role is the aforementioned phylogeographic break south of the Biobío River in the northern limit of Araucanía. However, such spatially concordant differentiation patterns could respond to very different times throughout the complex geological and climatic history of a sum of both new and old barriers. It also seems interesting the evaluation of the probable role of the numerous rivers arranged latitudinally in Chile, which in interaction with the relief seem to have been relevant in the case of lizards (Muñoz-Mendoza et al. 2017; Torres-Pérez et al. 2009). Finally, and far from exhausting the options for hypotheses, the questions about simultaneous multispecies processes of population retraction and recolonization in the glaciated range are pending. All these questions should be addressed, beyond verifying topological congruences, using coalescent approximations (ABC), which would allow us to estimate whether spatial patterns of diversity have been generated at similar times or have obeyed differentiated events in time. It is also necessary to incorporate multilocus evaluations, ideally through NGS methods, in order to base conclusions on a broad genomic coverage.

## 10.4 Phylogeography and Lizard Conservation

Biodiversity conservation initiatives should pay attention to all levels of organization, including genetic diversity and intraspecific lineages, so as to ensure the persistence of viable populations and to ensure their evolutionary and adaptive potential (Rodrigues and Gaston 2002). Until now, reality is far from this, and the greatest effort has been made to maximize species richness and endemism (Purvis and Hector 2000; Ricklefs and Schluter 1993). From this point of view, phylogeography contributes mainly in two aspects: first, detecting intraspecific diversity and its geographical distribution, which is fundamental for prioritizing territorial units of conservation, and second, understanding the history and factors that have generated intraspecific diversity. The latter is fundamental because understanding the past can be of great help to infer the future behavior of populations in the face of ongoing environmental changes. For example, one of the key aspects that could be affecting the populations of lizards is the change in land use (Chap. 14). The performance of some *Liolaemus* depends on the type of vegetation (Fuentes and Jaksić 1980; Medel et al. 1988), and the anthropogenic changes of vegetational structure could be significantly altering their behavior, abundance, and distribution (Mora and Labra 2017; Rubio and Simonetti 2011; Uribe and Estades 2014; Chap. 5). An example about this is the revision of the historical distribution of *L. pictus*, whose geographical range would have been considerably reduced (Vera-Escalona et al. 2010), as a probable consequence of the elimination and fragmentation of the native forest (Echeverria et al. 2006; Armesto et al. 2010). In this case, we do not know which intraspecific lineages became extinct during this process.

One of the phylogeographic paradigms states that areas of greater genetic diversity would be associated with scenarios with higher historical environmental stability (Carnaval et al. 2009), which apparently also extends to the richness of species (Werneck et al. 2012). The foregoing seems to be the case of the Chilean Mediterranean area, where, unlike the southern zone most affected by the glacial cycles, its populations would have experienced smaller distributional changes and fewer reductions in their abundances. If we consider an estimate of genetic conservation value (GCV) based both on genetic diversity and haplotype singularity (Fig. 10.11), those areas with the greatest GCV should be prioritized. According to estimates of the geographical distribution of this index in three *Liolaemus*, a large part of this diversity is concentrated in the unprotected Mediterranean zone. On the other hand, a trend toward lower values of this indicator has been observed in areas where glaciations have shown signs of impoverishment and genetic homogenization. A good example of this pattern is the geographic distribution of GCV in *L. pictus* (Fig. 10.11).

Previous detection of cryptic diversity in *Liolaemus* (e.g., Olave et al. 2017; Torres-Pérez et al. 2009), and the recent description of new species for Chile (Esquerré et al. 2013; Troncoso-Palacios et al. 2015, 2016), suggests that a large part of the diversity of lizards is not yet known for southern South America. In this sense, phylogeography is contributing much to the complex process of delimiting species. An example of phylogeographic evidence with consequences for the conservation of a lizard in Chile is the confirmation that the northern populations of *L. pictus* (currently *L. septentrionalis*) should be considered as a different species with a need to conserve. Something similar is the case of the *L. pictus* lineage of Isla Grande de Chiloé, although in this case it is a subspecies. For Chilean herpetozoans, the spatial delimitation of evolutionary conservation units (ESUs; Crandall et al. 2000; Moritz 1994) has been explicitly evaluated only for one species of snake (Sallaberry-Pincheira et al. 2011), while for lizards this aspect has only been collaterally commented in phylogeographic studies. For example, an interesting number of lineages have been detected in the northern central range of distribution of *L. tenuis* and *L. lemniscatus*, most of them in the Mediterranean area with the largest human population and the largest alteration of the landscape. This is a paradox in conservation because the coverage of the National System of Protected Areas (SNASPE) in Chile, which tends to increase toward the south of the country

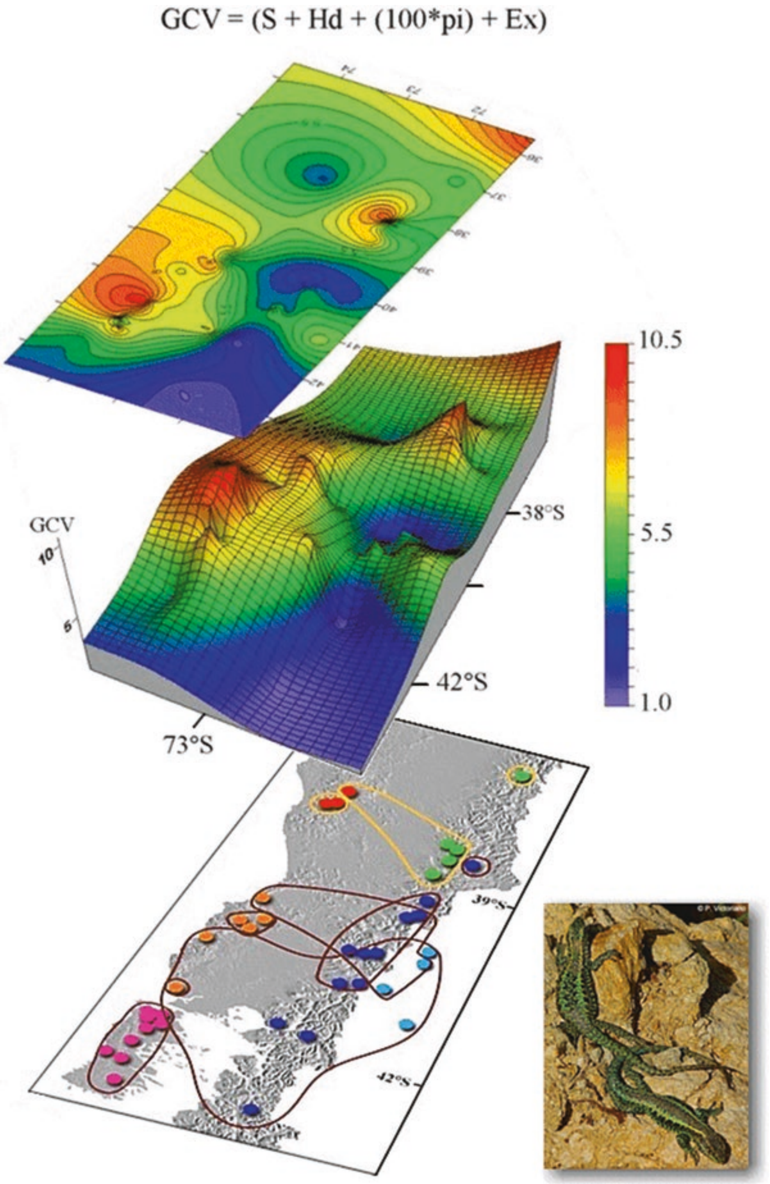

**Fig. 10.11** Geographic distribution of genetic conservation values (GCV) for the lizard *L. pictus*. The geographical distribution of lineages is also shown. *S* haplotype richness, *Hd* haplotype diversity, *pi* nucleotide diversity, and *Ex* number of private haplotypes

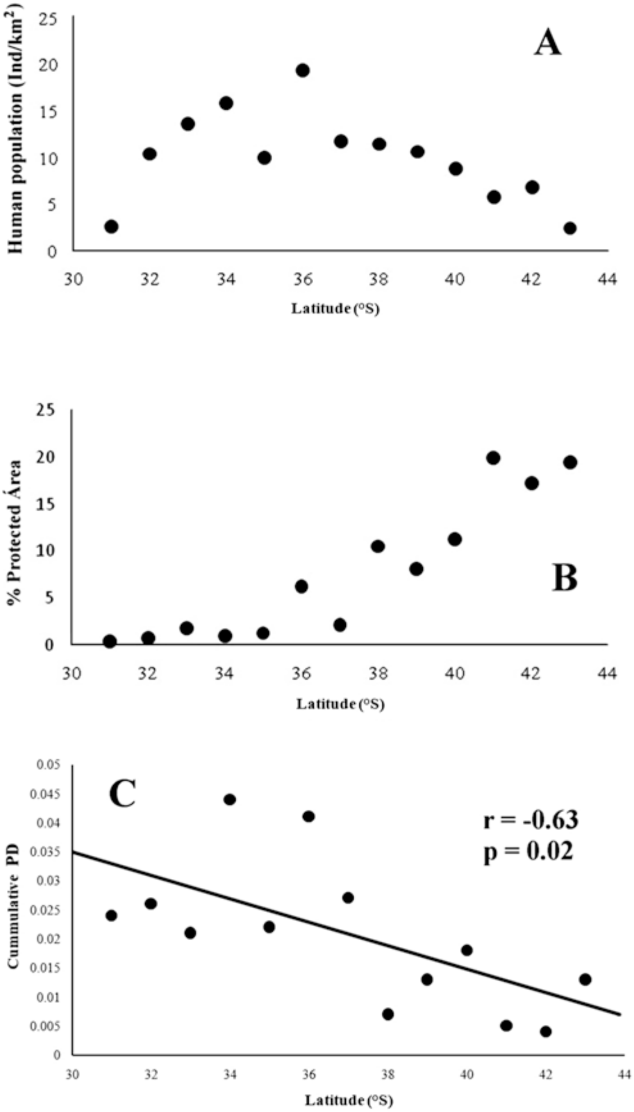

**Fig. 10.12** Latitudinal trends of (**a**) human population density and (**b**) of protected areas surface in central-southern Chile. In the bottom (**c**), the correlation of the accumulated phylogenetic diversity for the lizards *L. tenuis*, *L. pictus,* and *L. lemniscatus* with latitude is shown

(Fig. 10.12b), would not be protecting much of the intraspecific diversity of central Chile.

Due to its high richness and endemism, as well as the high and progressive degree of anthropic intervention, central-southern Chile is considered as one of the 25 hot spots of terrestrial biodiversity (Myers et al. 2000; Smith-Ramírez 2004). One criterion for prioritizing conservation areas is the evolutionary or phylogenetic diversity index (PD; Faith 1992). According to this criterion, those areas that include a higher genealogical diversity (probably generated over a longer evolutionary time) should be considered as more valuable. Taking this into an intraspecific context, when looking at the geographic tendencies of DF in three species of *Liolaemus* from central-southern Chile, a negative correlation of this index was observed with latitude (Fig. 10.12c) (Victoriano et al. 2012). In this regard, the quantification of the intraspecific phylogenetic diversity of lizards that would be protected within the SNASPE and the estimation of the percentage that is exposed to be eliminated are still pending. This kind of estimate was made for the amphibian *Telmatobius marmoratus* in northern Chile, where it was evident that a large part of its evolutionary diversity is unprotected (Victoriano et al. 2015). On the other hand, according to phylogeographic evidence, species of *Liolaemus* have been sensitive to the climatic changes of the past, which suggests that they are exposed to important negative consequences as a result of the ongoing anthropogenic climate change. The substantial difference between the natural processes of the past and those induced by humans is that the latter are occurring at a speed incompatible with the evolutionary response capacity of the species. A considerable number of lizard populations in the world have already become extinct due to global warming and, according to complex models, for the near future many of them have a high probability of disappearing, including Chilean *Liolaemus* populations (Sinervo et al. 2010). A useful initiative in this sense would be the overlap of phylogeographies with extinction probability maps, which could provide us with an idea of how much and what intraspecific evolutionary diversity could go extinct in the coming decades. A comparable approach is proposed by Brown et al. (2016), which aims to predict the genetic consequences of climate change, integrating coalescent approaches, spatiotemporal variations of demography, and estimates of landscape changes. Although classical molecular methods can still contribute much to the conservation of lizards, with the increasingly frequent use of genomics (NGS), more sophisticated options open up, for example, the use of the transcriptome, SNPs, and evaluation of loci with adaptive value. However, the direct application of genomics in the field of conservation is still in early development (McMahon et al. 2014).

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