



Emerging phylogeographical patterns of plants and terrestrial vertebrates from Patagonia

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Phylogeographical inferences, applied in a comparative framework across multiple species at a regional scale, provide the means for detecting regional and landscape-level patterns of biodiversity, which are important for understanding macroecology and evolution in a geographical mosaic against a backdrop broadly impacted by geological events. Although information on Patagonian phylogeographical patterns has accumulated for both aquatic and terrestrial organisms in recent years, no attempt has been made to compare patterns across major organismal groups. In this review, we compiled studies on the phylogeography of co-distributed plants and terrestrial vertebrates from Patagonia. From each study, we extracted information on levels of genetic diversity, and inferred demographic processes and phylogeographical breaks, as well as on putative refugia, to produce the first summary of emerging phylogeographical patterns for this region. This review reveals some congruent phylogeographical patterns within and among plants and terrestrial vertebrates, and suggests that Pre-Quaternary as well as Quaternary geological events would have been important driving forces in the evolutionary history of Patagonian lineages. Different processes and directional range shifts suggest a mosaic of phylogeographical patterns, far more complex than the several north–south common patterns traditionally proposed. © 2011 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2011, **103**, 475–494.

ADDITIONAL KEYWORDS: biogeography – comparative phylogeography – demographic processes – genetic diversity – glacial refugia – Patagonian mammals – Patagonian reptiles – Patagonian plants – Pleistocene glaciations – Pre-Quaternary processes.

Las inferencias filogeográficas, dentro de un marco comparativo cuando incluyen varias especies a escala regional, permiten detectar patrones de biodiversidad regional y de paisaje (fisonómicos), importantes para entender tanto la macroecología como el impacto a gran escala de los eventos geológicos. En los últimos años, el conocimiento filogeográfico de Patagonia se ha acumulado para organismos acuáticos y terrestres, y aunque se han propuesto pocos patrones demográficos o espaciales cualitativamente concordantes, no se ha hecho ningún intento de revisar comparativamente algunos de esos patrones considerando grandes grupos de organismos. En esta revisión compilamos el conocimiento publicado sobre la filogeografía de plantas vasculares y vertebrados terrestres de Patagonia con el propósito de comparar niveles de diversidad genética, procesos demográficos, quiebres filogeográficos y localización de posibles refugios, para producir el primer resumen de patrones filogeográficos emergentes

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para esta región. Esta revisión revela algunos patrones filogeográficos congruentes dentro y entre plantas vasculares y vertebrados terrestres, y sugiere que tanto los eventos geológicos Cuaternarios como los pre-Cuaternarios pudieron haber jugado un papel importante en la historia evolutiva de los linajes patagónicos. Diferentes procesos y cambios direccionales en los rangos de distribución, sugieren un mosaico de patrones filogeográficos mucho más complejo que los patrones norte-sur tradicionalmente propuestos.

PALABRAS CLAVE: biogeografía – filogeografía comparada – procesos demográficos – diversidad genética – refugios glaciales – mamíferos de Patagonia – reptiles de Patagonia – plantas de Patagonia – glaciaciones Pleistocénicas – procesos Pre-Cuaternarios.

INTRODUCTION

Phylogeography is an integrative field of science linking micro- and macroevolutionary processes (Bermingham & Moritz, 1998). By combining analyses of current population genetic structure with organismal distributions and historical changes in the environment, phylogeography provides the means for making strong inferences regarding dispersal, speciation, extinction, and other population-level processes. Applied in a comparative framework across multiple species at a regional scale, phylogeographical inference enables the detection of regional and landscape-level patterns of biodiversity important for understanding macroecology, broad impacts of geological events, and areas of high conservation priority (Bermingham & Moritz, 1998; Moritz, 2002).

Among inhabited continents, South America exhibits the greatest void in phylogeographical knowledge, with only 6.3% of relevant articles published worldwide from 1987 to 2007 dedicated to organisms of this continent (Beheregaray, 2008). Unlike temperate regions of North America and Europe, where considerable effort has focused on phylogeny reconstruction within and among species, very little is known about the phylogeography of temperate South America. Patagonia, the southernmost area of this continent, is among the least studied regions phylogeographically, and yet arguably has been impacted more than other areas of South America by environmental changes, both recent and over geological time scales (Rabassa, 2008a).

Over the past several million years, glaciations and associated climate change, tectonics with volcanism, palaeobasins, and seashore shifts with marine incursions have dramatically altered the landscape of Patagonia (Ramos & Ghiglione, 2008; Martínez & Kutschner, 2011; Ponce *et al.*, 2011). The numerous glacial advances and retreats during the Pleistocene are also well known (Rabassa, Coronato & Martínez, 2011). For example, the Greatest Patagonian Glaciation (GPG; 1.2 to 1.0 Mya) and the Last Glacial

Maximum (LGM; 20 to 18 kya) differed both in extent and duration. The ice sheet extent during the GPG was significantly greater than that during the LGM and the last several glaciations (McCulloch *et al.*, 2000; Ponce *et al.*, 2011); thus, these events most likely differentially impacted the abundance and distribution of the local biota.

In recent years, Patagonian phylogeographical knowledge has been accumulating for both aquatic and terrestrial organisms (e.g. marsupials: Himes, Gallardo & Kenagy, 2008; rodents: Kim *et al.*, 1998; Lessa, D'Elia & Pardiñas, 2010; lizards: Morando *et al.*, 2003, 2004, 2007; Avila, Morando & Sites, 2006; fishes: Cussac *et al.*, 2004; Ruzzante *et al.*, 2006; crabs: Xu *et al.*, 2009; gymnosperms: Premoli, Kitzberger & Veblen, 2000; Pastorino & Gallo, 2002; Acosta & Premoli, 2010; Angiosperms: Muellner *et al.*, 2005; Jakob, Martínez-Meyer & Blattner, 2009; Cosacov *et al.*, 2010). Most of these studies focused on one or few taxa and, although a few qualitatively concordant demographic or spatial patterns have been proposed for rodents (Lessa *et al.*, 2010), lizards (Morando *et al.*, 2007; Victoriano *et al.*, 2008), fishes (Ruzzante *et al.*, 2008; Zemlak *et al.*, 2008), and plants (Pastorino *et al.*, 2009; Cosacov *et al.*, 2010), no attempt has been made to review some of these patterns comparatively across major organismal groups.

Importantly, shared biogeographical patterns alone are insufficient for inferring causal mechanisms. Similar concordant patterns may result from different underlying causal factors operating over different times (i.e. pseudocongruence; Soltis *et al.*, 2006). However, if diverse taxa with variable natural histories and surveys based on different kinds of genetic markers produce qualitatively congruent phylogeographical patterns, then it is likely that the geological and environmental history of a certain region produced similar impacts on the regional biota. Building upon single-species analyses, the first step in comparative phylogeography is to determine whether qualitatively congruent patterns exist among taxa that can serve as initial hypotheses. These hypoth-

eses can further be tested with independent data, new analyses, and rigorous comparative statistical frameworks (Knowles, 2004; Carstens & Richards, 2007; Knowles & Carstens, 2007; Hickerson *et al.*, 2010).

The goal of the present study is to review and summarize current knowledge about the phylogeography of plants and terrestrial vertebrates from Patagonia. We compare levels of genetic diversity, inferred demographic processes, phylogeographical breaks and putative refugia to produce the first regional summary of emerging phylogeographical patterns and past scenarios for this region.

MATERIAL AND METHODS

Patagonia is defined here as the region extending south of the Río Colorado (approximately 35°S to 36°S) in Argentina, and in Chile, south of Valdivia (approximately 39°S) to the southernmost point of South America (56°S). This area includes two main geographically distinct units. First, the Patagonian steppe is a large, dry, extra-Andean plain covered by grassland and scrubby vegetation that extends from the eastern slopes of the southern Andes to the Atlantic coast, and a small portion of Chile (between 36°S and 43°S). This extension includes two main phyto-geographical provinces: the Monte Province which extends from central-northern Argentina to north-eastern extra-Andean Patagonia, reaching 43°S and the Patagonian Province which stretches over the remaining extra-Andean extensions. The second unit, the Andean region, is much smaller and runs along the Andes from 37°S to the southernmost Magellan and Fuegian Archipelagos. This unit contains two main phyto-geographical provinces: the Sub-Antarctic province which comprises different forest types on the eastern and western slopes of the Andes and several units of grassy steppes, and the Alto-Andean province which occupies the highest mountains between 1600 and 600 m a.s.l. (Coronato *et al.*, 2008).

We compiled all published phylogeographical studies of Patagonian plants and terrestrial vertebrates. A few other studies, not specifically of a phylogeographical nature (e.g. isozymes studies) but that also provide information on genetic diversity in a geographical and historical context, were also included. We searched in the Web of Science for all articles that contained in the title, abstract, or keyword the following terms: 'Patagonia phylogeography', 'Patagonia Pleistocene glaciations', 'glacial refugia Patagonia', and 'South America biogeography'.

From each paper, we recorded the following information: geographical coordinates, number of sampled sites (localities), number and type of molecular markers, geographical extension, species range coverage, type and location of phylogeographical

breaks, hypothesized refugia, secondary contact areas, inferred demographic processes by area and divergence times (if available).

SAMPLING COVERAGE

To summarize the sampling locality coverage, all localities were mapped using the point-to-grid richness analysis tool in DIVA-GIS (Hijmans *et al.*, 2001), using a $0.1667 \times 0.1667^\circ$ grid (i.e. 18×18 km at the equator), and applying the circular neighborhood option with a 1° (111 km) diameter. We made two maps (plants and vertebrates) from the complete dataset; and four additional maps were made to focus solely on lizards, rodents, woody plants, and perennial herbs.

REFUGIA AND BREAKS

We recorded the type and geographical distribution of hypothesized refugia (i.e. *in situ* persistence during Pleistocene glaciations) for each species. Some of these were explicitly mentioned as such in the original papers, whereas others were more subtly mentioned, mainly in the discussion sections. Generally, studies have recognized refugia based at least on one (and often on several) of the following criteria: restricted areas with the presence of exclusive haplotypes/alleles, shared haplotypes/alleles between potential refugia and recolonized areas, and high genetic diversity. Based on their geographical localization we classified glacial refugia into the following types: peripheral and lowland (*sensu* Holderegger & Thiel-Egenter, 2009) and valley refugia (i.e. patchy refugia produced by Alpine valley Glaciations; Rabassa & Clapperton, 1990). We also compiled information on geographical genetic discontinuities to summarize phylogenetic breaks.

GENETIC DIVERSITY

Geographical distributions of genetic diversity were explored within each principal organismal group (i.e. plants and vertebrates) and in combination. Diversity indices per population (in plants) or clade (in vertebrates) were standardized and scaled from 1–100 within each species. We selected whether the haplotype diversity index or its equivalent for diploid data, the expected heterozygosity. In studies where diversity indices were not shown for each population or clade but information was available, we calculated gene diversity following the formula proposed in the ARLEQUIN software manual (p. 90; Excoffier, Laval & Schneider, 2005). Estimated genetic diversity for each group of organism (i.e. plants and vertebrates) was mapped using the point-to-grid statistical analy-

sis tool in DIVA-GIS (Hijmans *et al.*, 2001), using the mean as the output variable. To avoid misinterpretations of the data, two different grid sizes of $0.1667 \times 0.1667^\circ$ and $1 \times 1^\circ$ (i.e. 18×18 and 111×111 km at the equator, respectively) and the circular neighborhood option with a 1° (111 km) diameter were applied. To determine shared areas of high, medium, and low diversity between plants and vertebrates, each grid was reclassified in three levels (dividing the observed values range in three equal intervals: low, medium, and high genetic diversity) and then multiplied using the option overlay in DIVA-GIS. As an alternative approach, each species grid was reclassified in three levels, dividing the observed values range in three equal intervals: low, medium, and high genetic diversity; for each group of organisms, we performed a stack of all the reclassified grid layers, and the genetic diversity for each group was mapped using the point-to-grid statistical analysis.

HISTORICAL EVENTS/PROCESSES

For information on events and processes, we recorded the population geographical coordinates associated with the inferred process. Processes inferred by each reviewed paper were compiled either from nested clade phylogenetic analyses (Templeton, Routman & Phillips, 1995; Templeton, 2004), mismatch distribution (Rogers, 1995), and neutrality tests (Tajima, 1989; Fu, 1997). We also considered inferences that were based on analyses of the geographical distribution of genetic diversity. We grouped inferences into four categories: demographic stability (extended isolated areas where presumably large panmictic populations persisted), demographic/range expansion (including long distance dispersion/colonization), secondary contact, and fragmentation (including allopatric fragmentation and restricted gene flow) defined as an area containing several spatially circumscribed haplogroups being differentiated by relatively large mutational steps under allopatric fragmentation; we considered also colonization routes that were suggested in the reviews based on the distribution of genetic diversity from putative source areas (with high genetic diversity) to areas of low diversity, and/or the presence of shared versus private haplotypes. For each group of organisms, populations with their associated inferences were mapped using DIVA-GIS. Polygons indicating different processes were traced using CorelDraw (Corel Corp.).

RESULTS

COMPILED PUBLICATIONS

A total of 33 publications were identified from the database search, 20 of which corresponded to plant

studies and 13 to terrestrial vertebrates. Almost all plant studies (90%) focused on a single species, whereas 53% of vertebrate publications included more than one taxon. On average, plant studies included considerably higher number of individuals than vertebrate studies, whereas the number of sampling localities is similar for both (Table 1). Studies performed on vertebrates are methodologically more homogeneous than the plant studies. The vertebrate studies all used mitochondrial DNA as the molecular marker whereas, in plants, isozymes followed by cpDNA were the two most common molecular markers (Table 1).

GEOGRAPHICAL SAMPLING COVERAGE

We tallied 1361 sampling localities (639 corresponding to terrestrial vertebrates and 722 to plants; Table 1). Sampling coverage overall species extended over the entire Patagonian region; however, sampling intensity varied when considering terrestrial vertebrates and plants separately (Fig. 1). Terrestrial vertebrates were more intensively and homogeneously sampled at mid latitudes (between 34° and 44° S), covering the steppe as well as the Andean regions (Fig. 1A). Within vertebrates, lizards were homogeneously sampled, except for the southernmost part of Patagonia where sampling was less intense (Fig. 1B). Rodents were not only more broadly, but also more heterogeneously sampled, with a partial gap on the Santa Cruz steppe (Fig. 1C).

Plants, on the other hand, were more heterogeneously sampled than vertebrates. They were most densely studied in the Andean region between 38° and 45° S, whereas the steppes of Río Negro and Chubut Provinces are almost unexplored (Fig. 1D). Considering woody plants and perennial herbs separately, woody species were exclusively sampled on the Andean forests, where they have been intensively studied around latitude 41° S (Fig. 1E). Perennial herbs were more heterogeneously sampled, with intensive sampling along the Andean range but only limited sampling on the steppe (Fig. 1F).

All reviewed studies on terrestrial vertebrates covered the entire (or nearly entire) extension of the known species geographical range. By contrast, only 48% of the plant studies covered the total distributional range of the focal species.

REFUGIA

We were able to extract information on putative refugial areas for both vertebrates and plants (Fig. 2 and Table 2). Although fewer in number for vertebrates (Fig. 2A), putative refugia were highly coincident with putative refugia proposed for plants (Fig. 2B). Overall, five refugial areas were distinguished, which

Table 1. Summary statistics over 33 publications referred to phylogeographical studies on plants and terrestrial vertebrates from Patagonia

Taxon	Species or complexes	Populations (localities)	Individuals	Populations/species or complexes, mean (range)	Individuals/species or complexes, mean (range)	Total	
Plants	24	722	12 735	31 (10–184)	535 (60–2 608)		
Animals	37	639	1 541	13 (2–41)	31 (4–144)		
Total	61	1 361	14 276	44 (10–184)	566 (60–2 608)		
Marker		cpDNA or mtDNA	Microsatellite	RAPD	AFLP	RFLP	Isozymes
Plants (N)							
Species or complexes		7	1	3	3	2	10
Markers		12	8	14	10	18	110
Markers/species or complexes, mean (range)		1.7 (1–3)	8	5 (3–11)	3 (3–4)	9 (2–16)	10 (2–21)
Animals (N)							
Species or complexes		37					37
Markers		1					1
Markers/species or complexes, mean		1					1
Total (N)							
Species or complexes		44	1	3	3	2	10
Markers		13	8	14	10	18	110
Markers/species or complexes, mean		1.1	1.2	1.3	1.2	1.4	3.1

*Total number of species studied with at least one marker.

†Mean number of markers studied per species for the whole data set.

cpDNA, chloroplast DNA; mtDNA, mitochondrial DNA; APDs, randomly amplified polymorphic DNA; AFLP, amplified fragment length polymorphism; RFLP, restriction fragment length polymorphism.

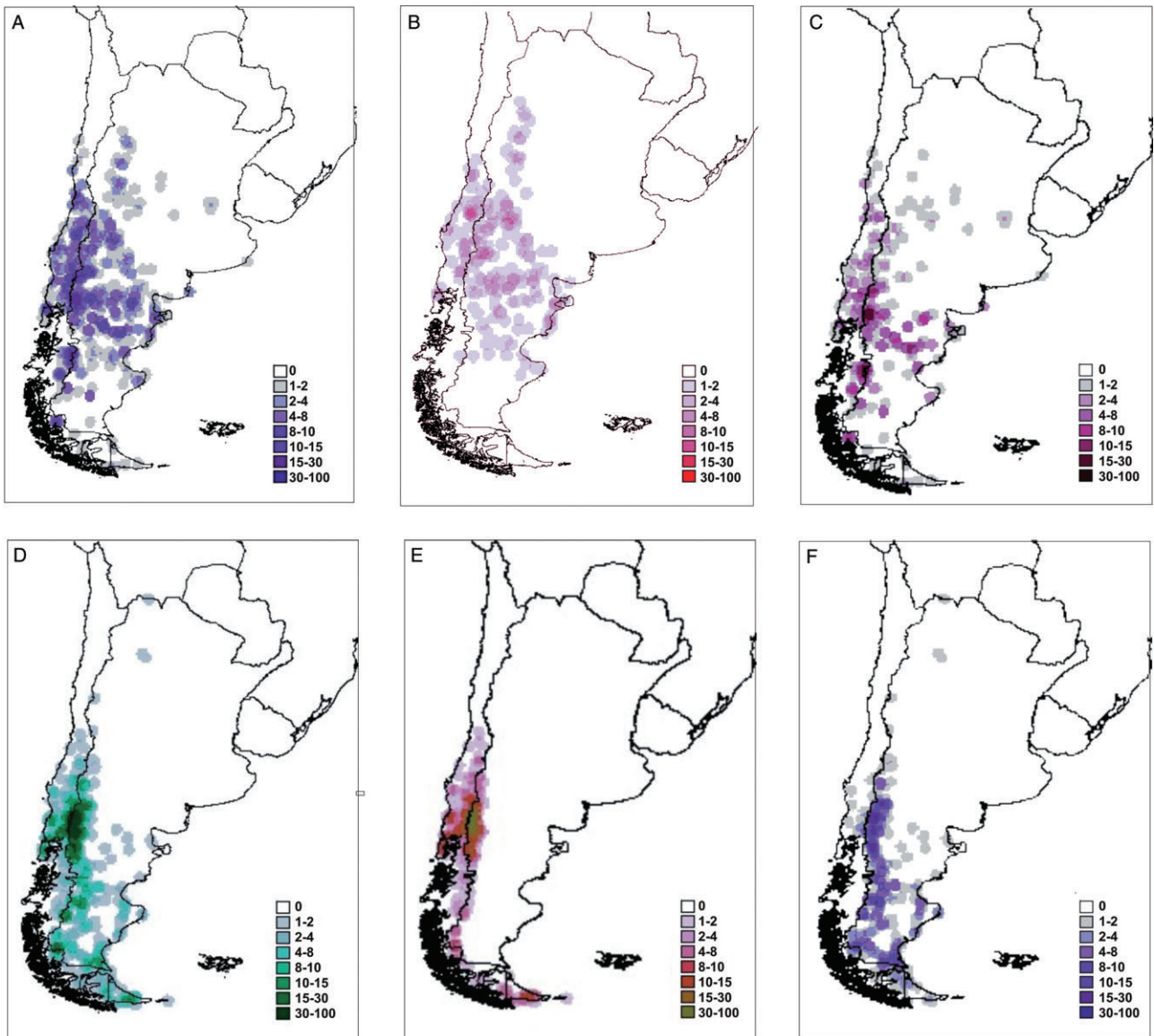


Figure 1. Geographical sampling coverage. Sampled localities for (A) terrestrial vertebrates; (B) lizard species; (C) rodent species; (D) plant species; (E) woody species; and (F) perennial herbs species. Colour scales indicate sampling density with an 18×18 km grid cell, darker colours correspond to higher density values.

we grouped into three categories (Fig. 2): 'lowland refugia', in the Chilean-Coastal range north of 42°S (a), in the coast of the San Jorge Gulf (approximately 46°S ; b) and in southern Patagonia (approximately 51°S to 53°S ; c); 'peripheral refugia', a longitudinal zone located along the eastern and western flanks of the Andes between 36°S and 53°S (d); and 'valley refugia', in the high-Andean region north of 36°S (e).

PHYLOGEOGRAPHICAL BREAKS

For terrestrial vertebrates, two phylogeographical breaks have been reported in the southern Central

Andes at 33°S (break 1, 1 sp.) and 35°S (break 2, 1 sp.), and a third one for the Coast of Central Chile at 38°S (break 3, 4 spp.). For the steppe area, six breaks were detected, four of them only for one species each, following approximately different river basins: Río Colorado (break 4), Río Negro (break 5), Río Limay (break 6), and the Río Chubut (break 7; Fig. 2A). The other two were concordant for two species each, one coincident with the Somuncurá plateau (break 8, 42°S), and the second located at 45°S (break 9, northern limit of the San Jorge Gulf). The southernmost break, coincident with the Magellan strait, was recorded for only one species (break 10; Fig. 2A).

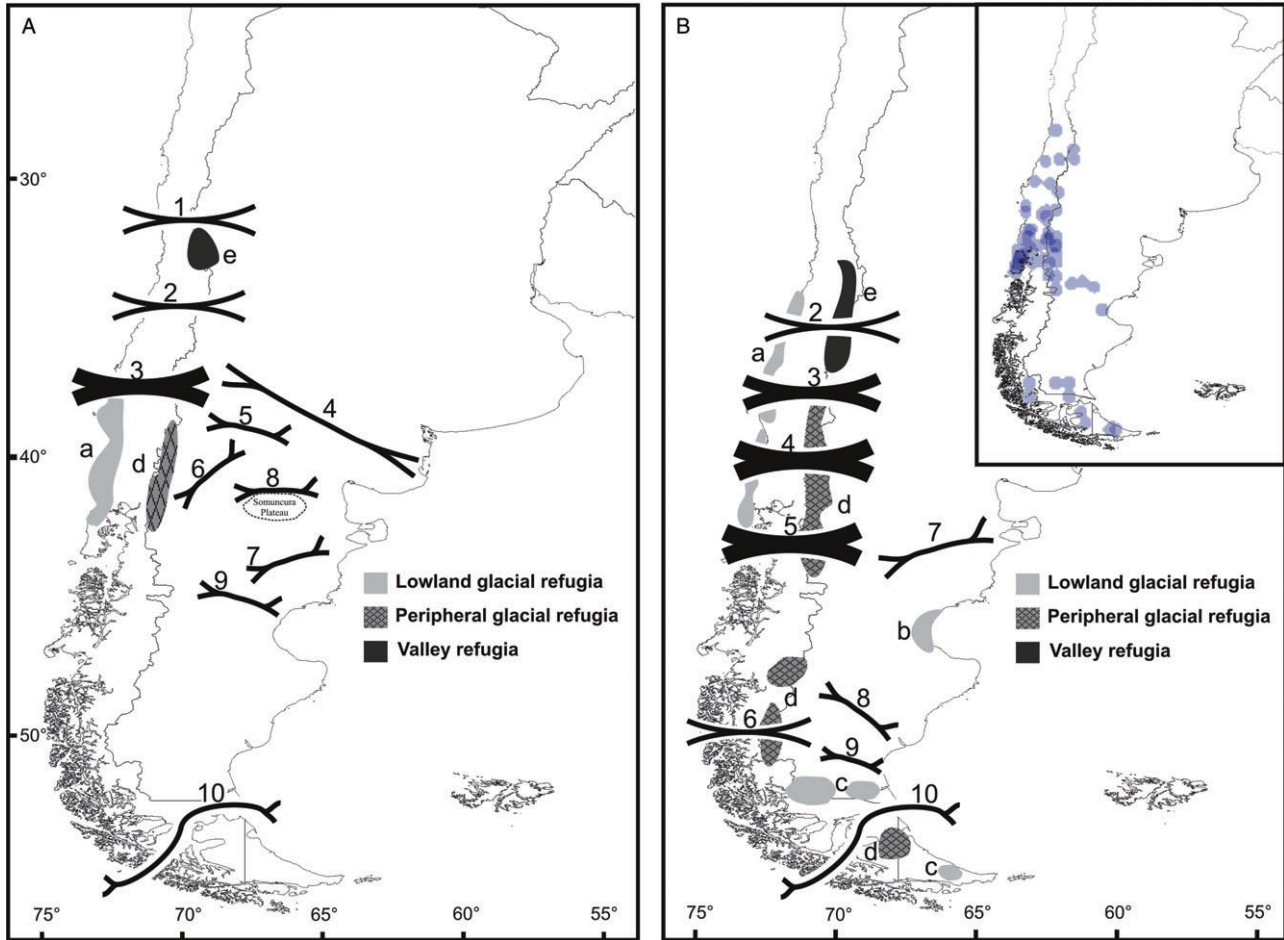


Figure 2. Phylogeographical breaks (lines and numbers) and hypothesized refugia (areas and letters) based on (A) terrestrial vertebrates data and (B) plants. Line thickness is in correspondence with the number of species for which the break was reported. Inset: refugia area density considering plants and animals combined. Colour scales indicate sampling density with an 18 × 18 km grid cell, darker colours correspond to areas inferred for a higher number of taxa.

For plants, breaks have been reported along the Patagonian Andes at approximately the following latitudes: 35°S (break 2, 1 sp.), 37.5°S (break 3, 3 spp.), 40.5°S (break 4, 5 spp.), 43°S (break 5, 5 spp.), and 50°S (break 6, 1 sp.). Across the Patagonian steppe, three breaks were detected for one species each, following approximately different river basins, from north to south: Río Chubut (break 7), Río Chico (break 8), and Río Coig (break 9). The southernmost break, detected for one species, was coincident with the Strait of Magellan (break 10; Fig. 2B).

Four phylogeographical breaks are shared between some vertebrate and plant taxa. Two are located in the Central Andean Region approximately at the same latitude (35°S and 37.5°S; breaks 2 and 3; Fig. 2), one at the Strait of Magellan (break 10) and another along the Chubut river basin (break 7; Fig. 2).

GENETIC DIVERSITY

Of the 20 plant studies, 17 (encompassing 640 sampling localities) included information regarding geographical patterns of genetic diversity. Diversity indices varied among studies with the two most common being expected heterozygosity and allelic richness. In vertebrates, 12 of the 13 studies (412 sampling sites) reported haplotype and nucleotide diversity indices for species or clades within them (see Appendix, Table A1).

In vertebrates, there were four main regions with high diversity (Fig. 3A): Chiloé Island, West-Chilean coast (north of 38°S), northern Neuquén and southern Mendoza Province in Argentina (35°S to 37°S) continuing southeast, following the Monte-Patagonia ecotone region, and the coastline of Rio Negro and Chubut Provinces in Argentina. Regions of low diversity were located along the Andean cordillera over almost the

Table 2. Location and type of putative glacial refugia proposed in the reviewed articles

Species	Type of refugium	Location	Extinct refugia	Reference
<i>Austrocedrus chilensis</i>	Peripheral glacial refugia	East & North of the Patagonian Andes		Arana <i>et al.</i> (2010), Pastorino & Gallo (2002)
<i>Calceolaria polyrhiza</i>	Peripheral glacial refugia Lowland glacial refugia Valley refugia	East of the Patagonian Andes Atlantic coast Southern-Central Andes	East of current Atlantic coastline	Cosacov <i>et al.</i> (2010)
<i>Embothrium coccineum</i>	Peripheral glacial refugia	East of the Patagonian Andes		Souto & Premoli (2007)
<i>Fitzroya cupressoides</i>	Peripheral glacial refugia Lowland glacial refugia	East & West of the Patagonian Andes West-Chilean coast		Allnutt <i>et al.</i> (1999), Premoli <i>et al.</i> (2000)
<i>Hordeum comosum</i>	Peripheral glacial refugia Valley refugia	East of the Patagonian Andes Southern-Central Andes		Jakob <i>et al.</i> (2009)
<i>Hordeum palustris</i> & <i>H. pubiflorum</i>	Lowland glacial refugia	South-East steppe		Jakob <i>et al.</i> (2009)
<i>Hypochoeris palustris</i>	Peripheral glacial refugia Lowland glacial refugia	East of the Patagonian Andes South-East steppe	East of current Atlantic coastline	Tremetsberger <i>et al.</i> (2009)
<i>Nothofagus obliqua</i>	Peripheral glacial refugia Lowland glacial refugia Valley refugia	East & North of the Patagonian Andes West-Chilean coast East & West of the Patagonian Andes West-Chilean coast Southern-Central Andes		Muellner <i>et al.</i> (2005)
<i>Nothofagus antarctica</i>	Peripheral glacial refugia	East of the Patagonian Andes		Azpilicueta <i>et al.</i> (2009)
<i>Nothofagus nervosa</i>	Peripheral glacial refugia	East, West & North of the Patagonian Andes		Pastorino <i>et al.</i> (2009)
<i>Nothofagus pumilio</i>	Lowland glacial refugia Peripheral glacial refugia Lowland glacial refugia Valley refugia	West-Chilean coast East of the Patagonian Andes West-Chilean coast & Tierra del Fuego Southern-Central Andes		Marchelli <i>et al.</i> (1998), Marchelli & Gallo (2001, 2006)
<i>Podocarpus nubigena</i>	Peripheral glacial refugia Lowland glacial refugia Lowland glacial refugia	East & North of the Patagonian Andes West-Chilean coast West-Chilean coast		Mathiasen & Premoli (2010), Premoli, Mathiasen & Kitzberger (2010)
<i>Abothrix olivaceus</i> <i>Abothrix olivaceus/xanthorhinus</i>	Lowland glacial refugia Lowland glacial refugia	West-Chilean coast West-Chilean coast		Quiroga & Premoli (2010)
<i>Dromiciops gliroides</i> <i>Liolaemus fitzingerii</i>	Lowland glacial refugia Lowland glacial refugia	West-Chilean coast Atlantic coast	East of current Atlantic coastline	Rodríguez-Serrano <i>et al.</i> (2006) Smith <i>et al.</i> (2001)
<i>Liolaemus tenuis/pictus/lemniscatus</i>	Lowland glacial refugia Peripheral glacial refugia	West-Chilean coast East of the Patagonian Andes		Himes <i>et al.</i> (2008) Avila <i>et al.</i> (2006)
<i>Loxodontomys micropus</i> <i>Phyllotis xanthopygus</i> <i>Sigmodontine rodents</i>	Peripheral glacial refugia Lowland glacial refugia Valley refugia	East of the Patagonian Andes Middle Patagonian Steepe Southern-Central Andes		Victoriano <i>et al.</i> (2008) Cañón <i>et al.</i> (2010) Kim <i>et al.</i> (1998) Lessa <i>et al.</i> (2010)

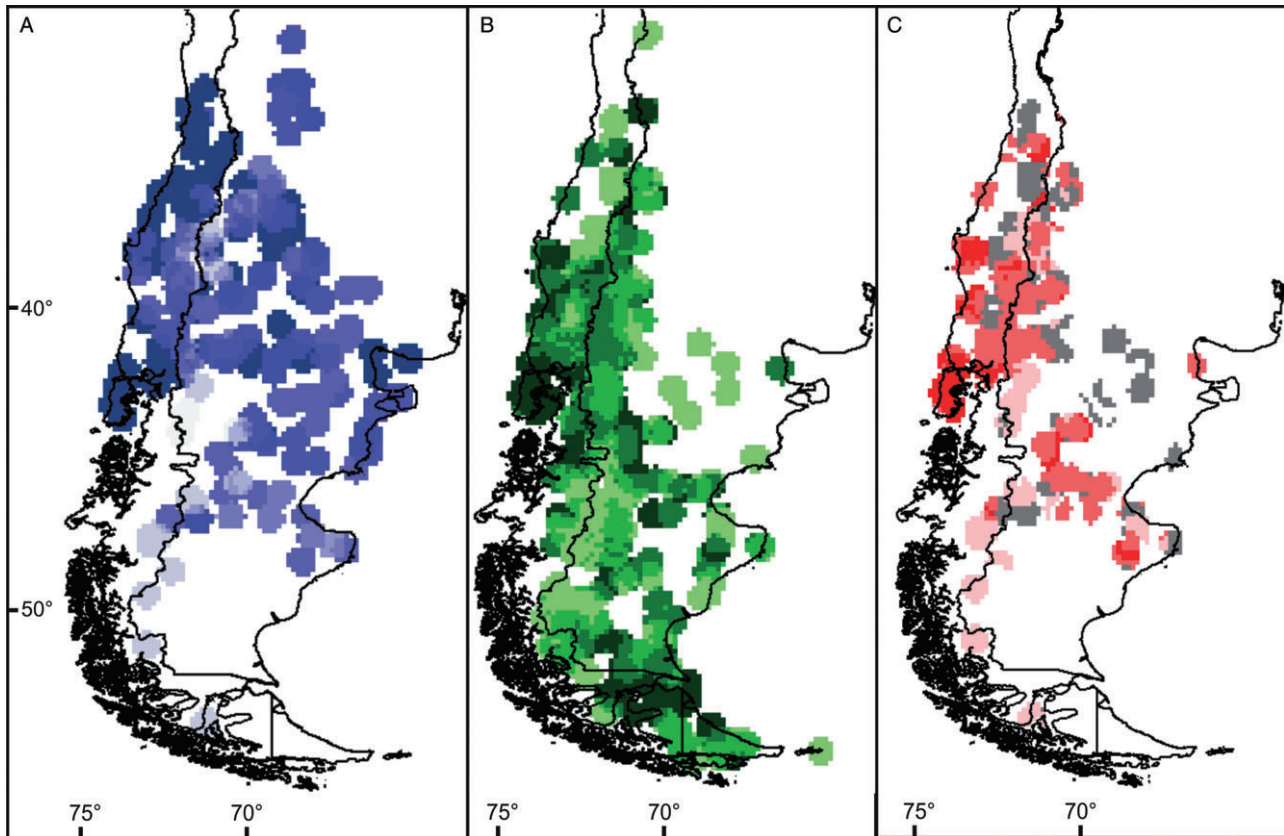


Figure 3. Geographical distribution patterns of genetic diversity. (A) terrestrial vertebrates; (B) plants; (C) terrestrial vertebrates and plants. Colour scales indicate genetic diversity values per an 18×18 km grid cell, darker colours correspond to higher genetic diversity values.

entire north–south axis of Patagonia (approximately 41°S to 52°S) in previously glaciated areas.

In plants, there were seven areas of high diversity (Fig. 3B): the West-Chilean coast (approximately 38°S to 42°S), southern Central Andes (approximately 35°S), northern Patagonian Andes (approximately 46°S), four areas covering all of the latitudinal extension of Patagonia located along a longitudinal transect of approximately 70°S (approximately 32°S , 39°S , 43°S , 49°S), central Patagonian steppe near the San Jorge Gulf (approximately 45°S to 46°S), southern San Jorge Gulf (approximately 47°S), and southernmost Patagonia and Tierra del Fuego (approximately 51°S to 53°S). Along the Atlantic coast, cells with intermediate values of genetic diversity predominate, whereas, towards the north-eastern region, cells with low diversity values are abundant. The regions of lowest diversity were located along the Andes cordillera over almost the entire foothill region of the southern Patagonian Andes (approximately 46°S to 52°S) in previously glaciated areas.

For plants and vertebrates combined (Fig. 3C), five regions with high levels of diversity were

identified: Chiloé Island, in the West-Chilean coast (approximately 40°S), in the southern Central Andes (approximately 35°S), in southwestern Chubut Province in the Patagonian steppe (approximately 46°S), and southern San Jorge Gulf (approximately 47°S). Three additional areas showed moderate to high levels of genetic diversity: one located in the West-Chilean coast (approximately 37°S , 39°S , and 42°S), in the northern Patagonian Andes (approximately 35°S to 38°S), and in Central Patagonia (approximately 45°S to 47°S) ranging from the eastern Andean flanks to the center of the Patagonian steppe. Three regions of low diversity were also identified: the Atlantic Coast (approximately 47°S), southern Patagonian Andes (approximately 46°S to 53°S), and the northern Patagonian Andes (approximately 37°S to 43°S). Areas where plants and vertebrates presented contrasting diversity values (high versus low) were also detected, with the most prominent region located in the transition zone between Patagonia and the Monte phytogeographical regions where animals seem to have high and plants low diversity (Fig. 3C).

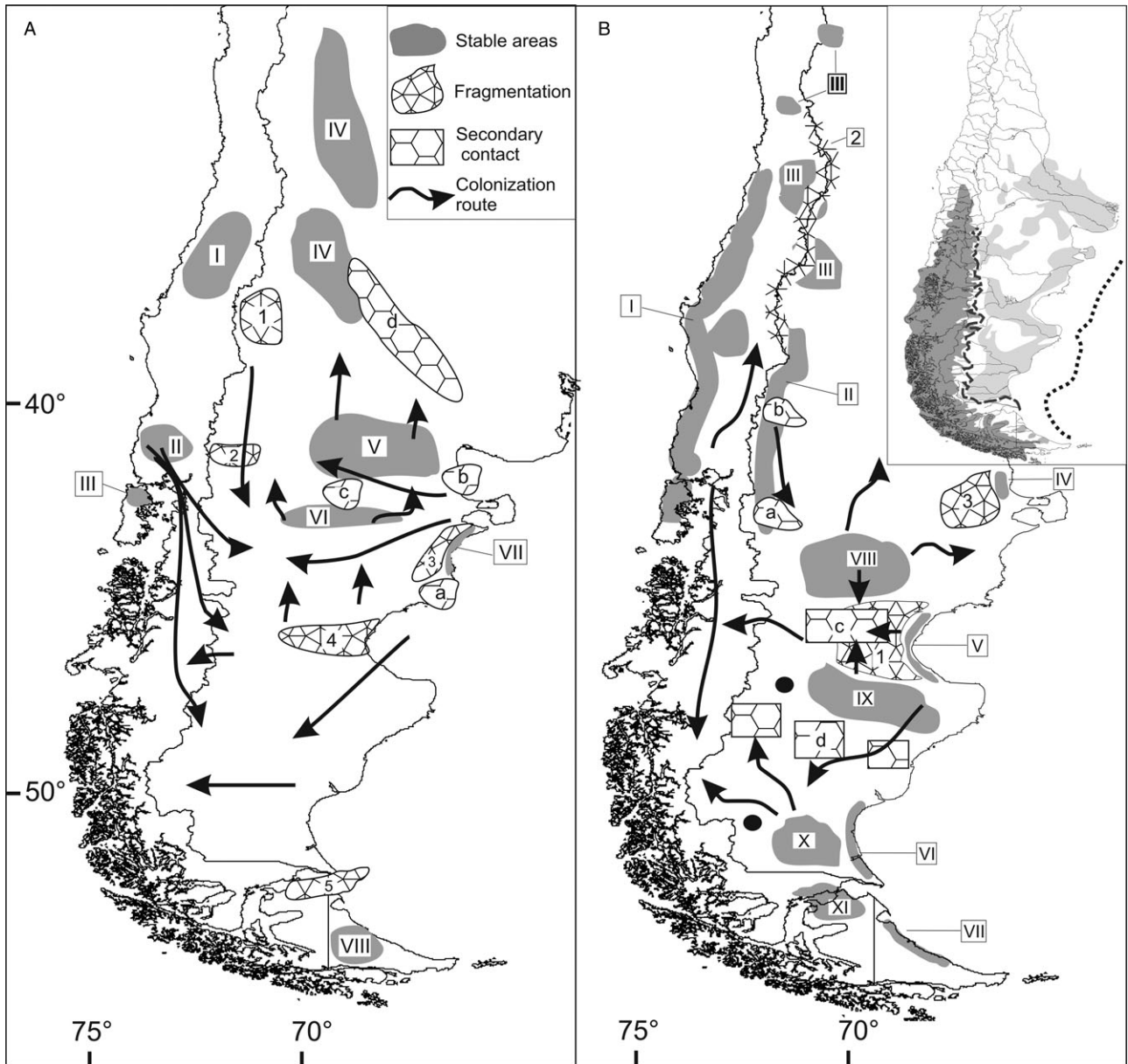


Figure 4. A, B, historical processes/events proposed for different areas of Patagonia. A, observed patterns in terrestrial vertebrates. B, observed patterns in plants. Black dots indicate disjunct haplotype distribution observes in three species.

HISTORICAL EVENTS/PROCESSES

For vertebrate taxa, five areas were identified associated with fragmentation inferences (Fig. 4A and Table 3): (1) northern Neuquén province, (2) southern Neuquén and northern Chubut provinces, (3) Sotomayor High Plateau in the eastern coastline of Chubut Province, (4) a strip west of the San Jorge Gulf, and (5) the Strait of Magellan. Stable areas as defined here are located in (I) Chile north of latitude approximately 36°S (II) at approximately 41°S and (III) north of Chiloé Island. In Argentina, stable areas within Patagonia are located on both sides of the Río Colorado (IV,

southern Mendoza and northern Neuquén), (V) northern Rio Negro, (VI) along a narrow east–west strip in northern Chubut, (VII) on Chubut northern coastline, and (VIII) in Tierra del Fuego (Fig. 4A). Several expansion routes have been inferred, some of them from the southern Chilean stable area southeast into Argentina and, in some rodent cases, reaching the southern tip of Santa Cruz Province. Southern expansion routes also have been proposed from the east towards the southwest at different latitudes. A third principal expansion has been proposed from northern Neuquén towards the south. Additional expansion routes, although with

Table 3. Demographic inferences reported for each taxon

	References	Taxon	RE	SC	FRA	S	CR
PLANTS	Bekessy <i>et al.</i> (2002)	<i>Araucaria araucana</i>				X	X
	Pastorino & Gallo (2002)	<i>Austrocedrus chilensis</i>	X			X	X
	Arana <i>et al.</i> (2010)	<i>Austrocedrus chilensis</i>	X		X	X	X
	Cosacov <i>et al.</i> (2010)	<i>Calceolaria polyrhiza</i>	X	X	X	X	X
	Souto & Premoli (2007)	<i>Embothrium coccineum</i>				X	X
	Premoli <i>et al.</i> (2000)	<i>Fitzroya cupressoides</i>				X	X
	Allnutt <i>et al.</i> (1999)	<i>Fitzroya cupressoides</i>					X
		<i>Hordeum comosum</i>				X	X
	Jakob <i>et al.</i> (2009)	<i>Hordeum patagonicum</i>	X		X	X	X
		<i>Hordeum pubiflorum</i>	X		X	X	X
	Tremetsberger <i>et al.</i> (2009)	<i>Hypochaeris incana</i>	X	X	X	X	X
	Muellner <i>et al.</i> (2005)	<i>Hypochaeris palustris</i>	X		X	X	X
	Pastorino <i>et al.</i> (2009)	<i>Nothofagus antarctica</i>			X	X	X
		<i>Nothofagus antarctica</i> ,		X			
	Acosta & Premoli (2010)	<i>Nothofagus betuloides</i> ,		X			
		<i>Nothofagus dombeyi</i> ,					
		<i>Nothofagus nitida</i> ,					
		<i>Nothofagus pumilio</i>					
	Marchelli <i>et al.</i> (1998)	<i>Nothofagus nervosa</i>	X			X	X
	Marchelli & Gallo (2004)	<i>Nothofagus nervosa</i>	X	X		X	
Marchelli & Gallo (2006)	<i>Nothofagus nervosa</i>	X			X	X	
Azpilicueta <i>et al.</i> (2009)	<i>Nothofagus obliqua</i>	X		X	X	X	
Mathiasen & Premoli (2010)	<i>Nothofagus pumilio</i>	X	X		X	X	
Premoli <i>et al.</i> (2010)	<i>Nothofagus pumilio</i>				X		
Premoli <i>et al.</i> (2001)	<i>Pilgerodendron uviferum</i>			X			
Quiroga & Premoli (2010)	<i>Podocarpus nubigena</i>				X	X	
TERRESTRIAL VERTEBRATES	Lessa <i>et al.</i> (2010)	<i>Abrothrix longipilis</i>	X			X	X
	Rodríguez-Serrano <i>et al.</i> (2006)	<i>Abrothrix olivaceus</i>	X			X	X
	Lessa <i>et al.</i> (2010)	<i>Abrothrix olivaceus</i>	X				X
	Smith <i>et al.</i> (2001)	<i>Abrothrix olivaceus/xanthrorhinus</i>	X	X		X	X
	Lessa <i>et al.</i> (2010)	<i>Akodon iniscatus</i>				X	
	Lessa <i>et al.</i> (2010)	<i>Calomys musculus</i>	X				
	Lessa <i>et al.</i> (2010)	<i>Chelemys macronyx</i>	X				
	Himes <i>et al.</i> (2008)	<i>Dromiciops gliroides</i>	X			X	X
	Lessa <i>et al.</i> (2010)	<i>Eligmodontia morgani</i>				X	
	Lessa <i>et al.</i> (2010)	<i>Eligmodontia typus</i>	X				
	Lessa <i>et al.</i> (2010)	<i>Euneomys chinchilloides</i>				X	
	Lessa <i>et al.</i> (2010)	<i>Geoxus valdivianus</i>				X	
	Lessa <i>et al.</i> (2010)	<i>Graomys griseoflavus</i>	X				
	Morando <i>et al.</i> (2007)	<i>Liolaemus bibronii</i>		X	X		
	Morando <i>et al.</i> (2003)	<i>Liolaemus buergeri</i>	X		X		X
	Avila <i>et al.</i> (2006)	<i>Liolaemus cuyanus</i>	X		X		X
	Morando <i>et al.</i> (2004)	<i>Liolaemus darwinii</i>	X	X	X		X
	Morando <i>et al.</i> (2003)	<i>Liolaemus elongatus</i>	X		X		X
	Avila <i>et al.</i> (2006)	<i>Liolaemus fitzingeri</i>	X	X	X		X
	Morando <i>et al.</i> (2007)	<i>Liolaemus gracilis</i>	X		X		
	Morando <i>et al.</i> (2004)	<i>Liolaemus grosseorum</i>	X	X	X		X
	Morando <i>et al.</i> (2003)	<i>Liolaemus kriegi</i>	X				X
	Victoriano <i>et al.</i> (2008)	<i>Liolaemus lemniscatus</i>			X	X	
	Avila <i>et al.</i> (2006)	<i>Liolaemus melanops</i>	X		X		X
	Morando <i>et al.</i> (2003)	<i>Liolaemus petrophilus</i>	X		X		
	Victoriano <i>et al.</i> (2008)	<i>Liolaemus pictus</i>			X	X	
	Morando <i>et al.</i> (2004)	<i>Liolaemus sp. nov.</i>	X	X	X		X

Table 3. *Continued*

References	Taxon	RE	SC	FRA	S	CR
Victoriano <i>et al.</i> (2008)	<i>Liolaemus tenuis</i>	X		X	X	
Avila <i>et al.</i> (2006)	<i>Liolaemus xanthoviridis</i>		X			
Lessa <i>et al.</i> (2010)	<i>Loxodontomys micropus</i>				X	
Cañón <i>et al.</i> (2010)	<i>Loxodontomys micropus</i>	X	X		X	
Lessa <i>et al.</i> (2010)	<i>Oligoryzomys longicaudatus</i>	X				
Palma <i>et al.</i> (2005)	<i>Oligoryzomys longicaudatus</i>	X				X
Kim <i>et al.</i> (1998)	<i>Phyllotis xanthopygus</i>	X			X	
Lessa <i>et al.</i> (2010)	<i>Phyllotis xanthopygus</i>	X				
Lessa <i>et al.</i> (2010)	<i>Reithrodon auritus</i>	X				
Ojeda (2010)	<i>Tympanoctomys barrerae</i>	X			X	X

RE, range expansion; SC, secondary contact; FRA, fragmentation; S, stable areas; CR, colonization routes.

a south–north direction from southern and northern Chubut and northern Rio Negro, have also been proposed (Fig. 4A). Some of these routes could be associated with the detected secondary contact areas on (a) the northern tip of the San Jorge Gulf, (b) on the coastline of Rio Negro Province, (c) in the central area of the Somuncurá Plateau, and (d) in the ecotone area between the Patagonia and Monte eco-regions (Fig. 4A).

In plants, three geographical regions affected by fragmentation processes were identified (Fig. 4B and Table 3): (1) central-eastern Patagonia, (2) Andean flanks north of 38°S, and (3) the north-eastern area of Patagonia in the transition between Patagonia and Monte phytogeographical provinces. In addition, a disjunct distribution of a haplotype could be detected in three species in south-western Santa Cruz province (Fig. 4B, black dots).

Areas where species may have persisted *in situ* have been proposed for eleven major regions: (I) Chilean-Coastal range north of 42°S and Chiloé island, (II) a longitudinal zone located in the eastern flanks of the Andes from 38°S to 42°S, (III) in scattered areas located in the high-Andean region north of 38°S, (IV) along the Atlantic coast of Rio Negro Province (approximately 41°S), (V) San Jorge Gulf (approximately 46°S to 47°S), (VI) Southern Santa Cruz (approximately 50°S to 52°S); and (VII) Tierra del Fuego (approximately 53°S); and also in inland Patagonia: (VIII) central Chubut Province, (IX) central northern Santa Cruz Province, (X) south-eastern Santa Cruz Province, and (XI) Tierra del Fuego (Fig. 4B). Secondary contact zones have been identified (a & b) on the eastern flanks of the Andes (c) in Central Patagonia (approximately 46°S) and (d) along a diagonal following the course of the Río Chico basin in Santa Cruz Province (approximately 48°S to 49°S; Fig. 4B). Recent demographic expansions have been hypothesized in all

reviewed studies and multiple directions have been proposed for them: from the east towards the south-west at different latitudes; with a north–south direction from southern Neuquén (approximately 39°S) and northern Chubut (approximately 42°S) along the Andes, and from south-eastern Chubut across the Steppe; additional expansion routes, but with a south–north direction from southern and northern Santa Cruz, southern Chubut, and southern Rio Negro Province, have been also proposed (Fig. 4B).

DISCUSSION

In this review of phylogeographical patterns for Patagonian terrestrial fauna and flora, we describe the location of potential glacial refugia and phylogeographical breaks, and areas of species expansion and colonization routes, some of which are consistent across a number of species; we also distinguish geographical areas within Patagonia in need of further research efforts. Indeed, the majority of focal plant taxa are Andean forest species with economic value (Pastorino & Gallo, 2002; Marchelli & Gallo, 2006; Acosta & Premoli, 2010; Arana *et al.*, 2010), with the exception of two non-woody steppe species (Tremetsberger *et al.*, 2009; Cosacov *et al.*, 2010). Increased research efforts are needed to broaden the taxonomic and geographical coverage of herbaceous Andean species, as well as woody Steppe species. Terrestrial vertebrate taxa are limited to mammals and lizards. Lizard studies have been based on denser sampling schemes in central and northern Patagonia, whereas mammal studies have typically included wider geographical coverage, although these are still scarce in the southernmost areas (Pardiñas *et al.*, 2011). Frogs have only recently begun to be studied in a phylogeographical perspective (Nuñez *et al.*, 2011).

GLACIAL REFUGIA

Populations with high genetic diversity suggest that they have either persisted for periods long enough for the maintenance of high genetic variation, or that the inhabited area was recolonized by a number of genetically distinct lineages from multiple refugia (Hewitt, 1996; Petit *et al.*, 2002; Mraz *et al.*, 2007). The presence of private haplotypes is crucial to distinguish between these alternatives (Pinceel *et al.*, 2005; Mraz *et al.*, 2007; Ronikier *et al.*, 2008; Huck *et al.*, 2009) because areas with low or null levels of within population genetic diversity but with private haplotypes suggest the existence of long lasting fragmented refugial areas.

The articles surveyed did not suggest a dramatic shift in species distributions during the LGM; a notable contrast with studies in northern continents (Pinceel *et al.*, 2005; Mraz *et al.*, 2007). Nevertheless, reported genetic patterns strongly support the existence of at least six stable areas where species survived during glaciations (i.e. east of the Patagonian Andes, northern Chiloé Island, northern Chilean Coast, Atlantic Coastline, northern Patagonia, and South of Santa Cruz Province and Tierra del Fuego). These areas show higher genetic diversity than areas where post-glacial colonization occurred, as in some areas of the southern Patagonian Steppe. Although vertebrate information is missing for most of the Santa Cruz Province, lizard data (Breitman *et al.*, 2011) identify high genetic diversity areas also demonstrated by plants.

Although more frequently documented in plants, putative refugial areas are also revealed in vertebrate phylogeographical patterns. Peripheral refugia were reported in 70% of the reviewed species (including at least one species each of woody and herbaceous plant, lizards, and rodents), indicating that, in Patagonia, the survival of species near the glaciers seems to be common (in contrast to the Northern Hemisphere; Hewitt, 2004; Pinceel *et al.*, 2005; Huck *et al.*, 2009). Regarding the location of peripheral refugia, the highest coincidence within and between groups was observed in the eastern foothills of the Andes between 39°S to 43°S, an area where the westerlies and associated precipitation peaks shifted to the north during LGM and back southward during interglacial periods; thus, humidity gradients were particularly produced in southern and northern Patagonia, whereas, at middle latitudes, moisture appeared more stable (Mancini *et al.*, 2005). An alternative non-exclusive explanation is that, at those latitudes, the ice sheet was confined to the peak summits with most of the foothill forests remaining unglaciated, thus allowing persistence of different taxa through later Quaternary climate shifts (Heusser, Heusser & Lowell, 1999).

Lowland refugia along the western Chilean Coast were the second most frequent in both vertebrate and plant studies (Victoriano *et al.*, 2008; Quiroga & Premoli, 2010). Less common but also coincident between taxa were lowland refugia along the Atlantic coastline, which today harbour remnants of a probably more extended easterly refugium that could have persisted on what is now the continental shelf, given that the coastline fluctuated in several longitudinal degrees to the east during glacial cycles (Ponce *et al.*, 2011). An interesting pattern found in all plant studies with sampling that covered the entire latitudinal range of Patagonia are the potential lowland refugia inferred as far as 51°S, both in the Andean and in Steppe areas, suggesting stable refugia at high latitudes (Jakob, Martínez-Meyer & Blattner, 2009; Tremetsberger *et al.*, 2009; Cosacov *et al.*, 2010; Mathiasen & Premoli, 2010). The existence of high genetic diversity, private haplotypes, together with the fact that all instances correspond to species with low dispersal capabilities, strongly suggests this shared pattern is the result of *in situ* persistence rather than a recolonization from northern refugia. Further supporting this hypothesis, divergent lineages with high genetic diversity within them have been found in lizards at these same latitudes (Breitman *et al.*, 2011). Less common are valley-type refugia north of 36°S, a region characterized by an Alpine valley-type glaciations (Rabassa, 2008b) that could have favoured the persistence of small, isolated populations (Himes *et al.*, 2008; Azpilicueta, Marchelli & Gallo, 2009; Cosacov *et al.*, 2010; Mathiasen & Premoli, 2010).

In summary, three salient common patterns in the geographical distribution of potential refugia could be retrieved from the available data: valley-type refugia north of 36°S, multiple concordance of peripheral refugia along the eastern foothills of the Andes between 39° to 43°S, and lowland refugia as far as 51°S.

PHYLOGEOGRAPHICAL BREAKS AND POSSIBLE PAST SCENARIOS

A number of geographical breaks are inferred from the genetic structure of Patagonian plant species (Tremetsberger *et al.*, 2009) and terrestrial vertebrates (Lessa *et al.*, 2010). For example, several studies suggest an association of many latitudinal breaks with the north to south range expansion of ancestral lineages (Jakob *et al.*, 2009; Cosacov *et al.*, 2010). The past geological and climatic events responsible for these breaks and their dating are uncertain; however, several kinds of potential barriers to gene flow have been suggested, including volcanic arches, ice sheets, palaeobasins, and terrain eleva-

tions (Morando *et al.*, 2004; Jakob *et al.*, 2009; Cosacov *et al.*, 2010; Mathiasen & Premoli, 2010).

Concordance in the distributions of divergent lineages or phylogroups among several Patagonian taxa appears to exist at a large spatial scale, although their temporal concordance is difficult to assess given that dating is susceptible to many sources of error, particularly if no fossil record is available for calibration. Of the surveyed studies, very few have calculated divergence times with a molecular clock (Cosacov *et al.*, 2010); instead, lineage divergence time was estimated in relation to the dating of major geological and climatological events. Unfortunately, the latter practice ties cause to effect rather than enabling independent dating of divergences, such as from molecular data.

In Patagonia, several scenarios have been hypothesized to explain lineage divergences, one of which invokes Pre-Quaternary processes such as tectonic/orogenic events, volcanism, and palaeobasins that may have driven some diversification in middle and northern Patagonia (Suárez & Márquez, 2007; Ramos & Ghiglione, 2008; Rabassa, 2008b). For example, a novel explanation for latitudinal breaks for *Nothofagus* species was proposed recently by Mathiasen & Premoli (2010), suggesting the influence of palaeobasins open to the Pacific during the Early–Middle Jurassic (165 to 145 Mya; Suárez & Márquez, 2007). However, this timing is not congruent with the evolutionary history and speciation timescale proposed for many other groups of Patagonian plants (Ezcurra, 2002; Jakob & Blattner, 2006; Jakob *et al.*, 2009; Nylinder *et al.*, 2010).

More recent Pre-Quaternary scenarios have been postulated for other breaks. For example, Cosacov *et al.* (2010) suggests that a break observed for *Calceolaria polyrhiza* in southern Mendoza may have been caused by the formation of a major landscape discontinuity (Ramos & Kay, 2006) during the uplifting of the Andes in the Late Miocene (11 Mya). A break at 37.5°S, observed for *Hypochoeris incana* (Tremetsberger *et al.*, 2009), *Nothofagus pumilio* (Mathiasen & Premoli, 2010) and three species of *Liolaemus* (Victoriano *et al.*, 2008) is concordant with the northernmost extension of the ice sheet during LGM; however, this break in *C. polyrhiza* (Cosacov *et al.*, 2010) was attributed to an area of extensive volcanic and tectonic activity during the Late Miocene (Ramos & Kay, 2006; Ramos & Ghiglione, 2008).

Miocene–Pliocene Andean orogeny and associated tectonic processes that occurred at 35° to 38°S may have had a major role in shaping the evolutionary history of many taxa. Indeed, several plant species or genera appear to have diversified in these northern areas and then migrated south and southeast, colonizing new niches that emerged concomitant with the

uplift of the Andes and the consequent desertification of the Steppe (Barreda, Guler & Palazzesi, 2008; Ramos & Ghiglione, 2008). This scenario was proposed for *C. polyrhiza* (Cosacov *et al.*, 2010), *Hordeum* (Jakob *et al.*, 2009) and *H. incana* (Tremetsberger *et al.*, 2009).

Within the younger scenarios temporally situated in the Quaternary Pleistocene glacial cycles, dynamics of the river basins, palaeobasins, and coastline shifts (Hernández, González & Hernández, 2008; Martínez & Kutscher, 2011; Ponce *et al.*, 2011) constitute possible factors that may have moulded the evolutionary history of the Patagonian lineages. Indeed, on the Patagonian Steppe, several breaks have been suggested to be concordant with river basins that currently drain (or that in the past drained) the Andean East watershed by crossing the steppe to the Atlantic Ocean. These include the following rivers: Río Colorado (*Liolaemus elongatus*; Morando, Avila & Sites, 2003), Río Neuquén (*L. elongatus*; Morando *et al.*, 2003), Río Limay (*Liolaemus bibronii*; Morando *et al.*, 2007), Río Chubut (*Phyllotis xanthopygus*; Kim *et al.*, 1998; *Hordeum*; Jakob *et al.*, 2009), Río Coig (*Hordeum*; Jakob *et al.*, 2009) and Río Chico (*C. polyrhiza*; Cosacov *et al.*, 2010). A rarely considered process in the Patagonian Steppe also could have molded biodiversity patterns such as Quaternary river basins that converted Patagonia into a highly fragmented landscape, as revealed today by extensive glaciofluvial gravel accumulations throughout the Steppe region revealing ancient powerful currents discharging to the sea (Martínez & Kutscher, 2011) (Fig. 4, inset).

Coastline shifts along the Atlantic could have promoted a vicariant pattern shared by three *Liolaemus* species at the northern and southern rim of the Somuncurá Plateau (Morando *et al.*, 2003, 2007; Avila *et al.*, 2006). When the coastline moved west, some populations migrated to the north, whereas others to the south of the Plateau promoting vicariance and reciprocal monophyletic haplogroups in these taxa.

Yet another break likely related to Quaternary processes is the Strait of Magellan, which was probably associated with coastline shifts during glacial cycles (Ponce *et al.*, 2011) and appears to have contributed to the genetic divergence in the plant genus *Hordeum* (Jakob *et al.*, 2009), and several Sigmodontine species (Lessa *et al.*, 2010; Pardiñas *et al.*, 2011). No historical events have been proposed for the 50°S break of *Hypochoeris incana* (Tremetsberger *et al.*, 2009) and for the 45°S break of *Liolaemus fitzingerii* and *Liolaemus xanthoviridis* (Avila *et al.*, 2006).

In summary, major genetic discontinuities in terrestrial Patagonian organisms follow a clear latitudinal pattern. These breaks, located along the Andes and on the steppe, appear to be the result of processes

operating at different temporal scales; the Andean breaks appear to be more ancient and likely associated with Pre-Quaternary processes (Andean orogeny and palaeobasins), whereas the more recent stepparian breaks are probably the result of Quaternary events such as glaciations cycles, as well as the associated variations in the dynamics of river basins and coastline shifts.

A target of future studies should be the inclusion of molecular clock calibrations based on fossils to elucidate ages of species divergent events, which may aid to discern if recent phylogeographical breaks only reflect geographical structuring with no underlying historical barriers.

PAST DEMOGRAPHY: RANGE EXPANSION AND COLONIZATION ROUTES

In some terrestrial vertebrate and plant studies, southward range expansion from Chubut to Santa Cruz Province was inferred along the eastern Patagonian Steppe (Avila *et al.*, 2006; Cosacov *et al.*, 2010; Lessa *et al.*, 2010; Pardiñas *et al.*, 2011), or southward and eastward in Chile (Smith, Kelt & Patton, 2001; Victoriano *et al.*, 2008). This pattern is consistent with the expected Pleistocene scenario where most plant communities migrated northwards during Pleistocene cold cycles, and later recolonized their habitats at higher latitudes when the climate warmed again (e.g. Markgraf, 1983). However, many species that show southward expansion also have a signal of persistence *in situ* in south-eastern Santa Cruz Province (Jakob *et al.*, 2009; Cosacov *et al.*, 2010), suggesting that the retraction was not homogeneous in the southern edge of the distribution range of some species.

Some northward expansions also occurred from central Santa Cruz to southern Chubut (Jakob *et al.*, 2009; Cosacov *et al.*, 2010) and from Chubut to northern Rio Negro Province (Morando *et al.*, 2004; Jakob *et al.*, 2009). Several instances of allopatric isolation followed by range expansion may have produced some of the areas of secondary contact we observe today, which are most probably of recent origin, after the GPG or LGM (Palma *et al.*, 2005; Azpilicueta *et al.*, 2009; Cosacov *et al.*, 2010; Lessa *et al.*, 2010). These secondary contact areas suggest that some species survived in more than one refugium, as previously proposed for the eastern Andes by Premoli (1998). Contact areas appear thus far not to be congruent between animals and plants. Variation in dispersal and differentiation rates among species may be responsible for the different location of most of these areas.

Although much work remains to be done, concordant dispersal routes support the expected outcome of

niche tracking following ice sheet fluctuations and climate change. Other concordant patterns suggest south–north expansions and *in situ* persistence in the southernmost areas. This may indicate that Pleistocene climate change and ice sheet fluctuations were not always the most direct factors acting on the demographic dynamics of Patagonian organisms, rather they acted in concert with other factors in more complex scenarios. It is noteworthy that several organisms presumably have remained isolated in patchy populations in the northern Andean area. Several non-mutually exclusive factors may explain this pattern such as the more intricate topography of the Andes favouring isolation among valleys and slopes, the narrow forested area which is more easily split into small areas, and the characteristic valley glaciation (Rabassa & Clapperton, 1990) that could have disrupted gene flow across valleys favouring local population persistence. Although there is lower incidence of fragmentation on the steppe, some aspects of its geological history (e.g. Quaternary palaeobasins, coastline shifts) allow us to expect that fragmentation might have taken place more often than has yet been detected.

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APPENDIX

Table A1. Lists of the 33 articles included in the present study

Reference	Taxon	Number of individuals	Number of sites	Markers	DI	Av
Bekessy <i>et al.</i> (2002)	<i>Araucaria araucana</i>	195	13	RAPD	Sh	D
Pastorino & Gallo (2002)	<i>Austrocedrus chilensis</i>	387	15	Isozymes	H_E	D
Arana <i>et al.</i> (2010)	<i>Austrocedrus chilensis</i>	448	14	Nuclear	H_E	D
Cosacov <i>et al.</i> (2010)	<i>Calceolaria polyrhiza</i>	590	68	cpDNA	H_D	D
Souto & Premoli (2007)	<i>Embothrium coccineum</i>	1020	34	AFLP	H_E	D
Premoli <i>et al.</i> (2000)	<i>Fitzroya cupressoides</i>	720	24	Isozymes	H_E	D
Allnutt <i>et al.</i> (1999)	<i>Fitzroya cupressoides</i>	89	12	RAPD	Sh	D
	<i>Hordeum comosum</i>	472	184	cpDNA (trnL-F)	H_D	C
Jakob <i>et al.</i> (2009)	<i>Hordeum patagonicum</i>	164		cpDNA (trnL-F)	H_D	C
	<i>Hordeum pubiflorum</i>	286		cpDNA (trnL-F)	H_D	C
Tremetsberger <i>et al.</i> (2009)	<i>Hypochaeris incana</i>	580	28	AFLP	–	–
Muellner <i>et al.</i> (2005)	<i>Hypochaeris palustris</i>	206	21	AFLP	Sh	D
Pastorino <i>et al.</i> (2009)	<i>Nothofagus antarctica</i>	60	12	cpDNA	–	–
Pastorino <i>et al.</i> (2009)	<i>Nothofagus antarctica</i>	674	12	Isozymes	H_E	D
	<i>Nothofagus antartica</i> ,			Nuclear	–	–
Acosta & Premoli (2010)	<i>Nothofagus betuloides</i> ,	~36	10	cpDNA		
	<i>Nothofagus dombeyi</i> ,					
	<i>Nothofagus nitida</i> ,					
	<i>Nothofagus pumilio</i>					
Marchelli & Gallo (2001)	<i>Nothofagus nervosa</i> / <i>Nothofagus obliqua</i>	1100	11	Isozymes	–	–
Marchelli & Gallo (2004)	<i>Nothofagus nervosa</i>	2608	20	Isozymes	–	–
Marchelli & Gallo (2006)	<i>Nothofagus nervosa</i>	125	26	RFLP	H_D	C
Marchelli <i>et al.</i> (1998)	<i>Nothofagus nervosa</i>		11	RFLP	–	–
Marchelli <i>et al.</i> (1998)	<i>Nothofagus nervosa</i>	100	10	cpDNA	–	–
Azpilicueta <i>et al.</i> (2009)	<i>Nothofagus obliqua</i>	154	27	AFLP	Ar	D
Mathiasen & Premoli (2010)	<i>Nothofagus pumilio</i>	204	41	cpDNA	H_D	C
Mathiasen & Premoli (2010)	<i>Nothofagus pumilio</i>	1181	59	Isozymes	–	–
Premoli <i>et al.</i> (2010)	<i>Nothofagus pumilio</i>	420	14	Isozymes	H_E	D
Premoli <i>et al.</i> (2001)	<i>Pilgerodendron wiferum</i>	600	20	Isozymes	H_E	D
Quiroga & Premoli (2010)	<i>Podocarpus nubigena</i>	352	14	Isozymes	H_E	D

Table A1. Continued

Reference	Taxon	Number of individuals	Number of sites	Markers	DI	Av
Lessa <i>et al.</i> (2010)	<i>Abrothrix longipilis</i>	21	20	mtDNA-cyt-b	H_D	D
Rodríguez-Serrano <i>et al.</i> (2006)	<i>Abrothrix olivaceus</i>	67	15	mtDNA-CR	H_D	D
Lessa <i>et al.</i> (2010)	<i>Abrothrix olivaceus</i>	72	44	mtDNA-cyt-b	H_D	D
Smith <i>et al.</i> (2001)	<i>Abrothrix olivaceus/xanthrorhinus</i>	26	21	mtDNA-cyt-b	H_D	D
Lessa <i>et al.</i> (2010)	<i>Akodon iniscatus</i>	14	11	mtDNA-cyt-b	H_D	D
Lessa <i>et al.</i> (2010)	<i>Calomys musculinus</i>	20	18	mtDNA-cyt-b	H_D	D
Lessa <i>et al.</i> (2010)	<i>Chelemys macronyx</i>	18	10	mtDNA-cyt-b	H_D	D
Himes <i>et al.</i> (2008)	<i>Dromiciops gliroides</i>	21	56	mtDNA-cyt-b	H_D	D
Lessa <i>et al.</i> (2010)	<i>Eligmodontia morgani</i>	17	14	mtDNA-cyt-b	H_D	D
Lessa <i>et al.</i> (2010)	<i>Eligmodontia typus</i>	30	20	mtDNA-cyt-b	H_D	D
Lessa <i>et al.</i> (2010)	<i>Euneomys chinchilloides</i>	13	9	mtDNA-cyt-b	H_D	D
Lessa <i>et al.</i> (2010)	<i>Geoxus valdivianus</i>	9	9	mtDNA-cyt-b	H_D	D
Lessa <i>et al.</i> (2010)	<i>Graomys griseoflavus</i>	21	13	mtDNA-cyt-b	H_D	D
Morando <i>et al.</i> (2007)	<i>Liolaemus bibronii</i>	110	41	mtDNA-cyt-b	H_D	D
Morando <i>et al.</i> (2003)	<i>Liolaemus buergeri</i>	18	6	mtDNA-cyt-b	H_D	D
Avila <i>et al.</i> (2006)	<i>Liolaemus cuyanus</i>	33	14	mtDNA-cyt-b	H_D	D
Morando <i>et al.</i> (2004)	<i>Liolaemus darwinii</i>	66	28	mtDNA-cyt-b	H_D	D
Morando <i>et al.</i> (2003)	<i>Liolaemus elongatus</i>	75	22	mtDNA-cyt-b	H_D	D
Avila <i>et al.</i> (2006)	<i>Liolaemus fitzingeri</i>	39	13	mtDNA-cyt-b	H_D	D
Morando <i>et al.</i> (2007)	<i>Liolaemus gracilis</i>	32	21	mtDNA-cyt-b	H_D	D
Morando <i>et al.</i> (2004)	<i>Liolaemus grosseorum</i>	28	9	mtDNA-cyt-b	H_D	D
Morando <i>et al.</i> (2003)	<i>Liolaemus kriegi</i>	26	8	mtDNA-cyt-b	H_D	D
Victoriano <i>et al.</i> (2008)	<i>Liolaemus lemniscatus</i>	52	14	mtDNA-cyt-b	H_D	D
Avila <i>et al.</i> (2006)	<i>Liolaemus melanops</i>	77	21	mtDNA-cyt-b	H_D	D
Morando <i>et al.</i> (2003)	<i>Liolaemus petrophilus</i>	39	14	mtDNA-cyt-b	H_D	D
Victoriano <i>et al.</i> (2008)	<i>Liolaemus pictus</i>	82	15	mtDNA-cyt-b	H_D	D
Morando <i>et al.</i> (2004)	<i>Liolaemus sp. nov.</i>	4	4	mtDNA-cyt-b	H_D	D
Victoriano <i>et al.</i> (2008)	<i>Liolaemus tenuis</i>	144	41	mtDNA-cyt-b	H_D	D
Avila <i>et al.</i> (2006)	<i>Liolaemus xanthoviridis</i>	35	10	mtDNA-cyt-b	H_D	D
Lessa <i>et al.</i> (2010)	<i>Loxodontomys micropus</i>	12	9	mtDNA-cyt-b	H_D	D
Cañón <i>et al.</i> (2010)	<i>Loxodontomys micropus</i>	87	26	mtDNA-cyt-b	H_D	D
Lessa <i>et al.</i> (2010)	<i>Oligoryzomys longicaudatus</i>	45	35	mtDNA-cyt-b	H_D	D
Palma <i>et al.</i> (2005)	<i>Oligoryzomys longicaudatus</i>	33	31	mtDNA-cyt-b	H_D	D
Kim <i>et al.</i> (1998)	<i>Phyllotis xanthopygus</i>	58	10	mtDNA-cyt-b	H_D	D
Lessa <i>et al.</i> (2010)	<i>Phyllotis xanthopygus</i>	15	14	mtDNA-cyt-b	H_D	D
Lessa <i>et al.</i> (2010)	<i>Reithrodon auritus</i>	14	13	mtDNA-cyt-b	H_D	D
Ojeda (2010)	<i>Tympanoctomys barrerae</i>	60	8	mtDNA-CR	H_D	D

Diversity index (DI) obtained from the respective article is indicated. Ar, allelic richness; Sh, Shannon index; H_E , expected heterocigosity; H_D , haplotype diversity. D, available in the revised article, C, calculated for the present study.