MOLECULAR ECOLOGY

FROM THE COVER

Genetic footprints of late Quaternary climate change in the diversity of Patagonian-Fueguian rodents

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Abstract

Species are impacted by climate change at both ecological and evolutionary time scales. Studies in northern continents have provided abundant evidence of dramatic shifts in distributions of species subsequent to the last glacial maximum (LGM), particularly at high latitudes. However, little is known about the history of southern continents, especially at high latitudes. South America is the only continent, other than Antarctica, that extends beyond 40 °S. Genetic studies of a few Patagonian species have provided seemingly conflicting results, indicating either postglacial colonization from restricted glacial refugia or persistence through glacial cycles and *in situ* differentiation. Using mitochondrial DNA sequences of 14 species of sigmodontine rodents, a major faunal ensemble of Patagonia and Tierra del Fuego, we show that at least nine of these species bear genetic footprints of demographic expansion from single restricted sources. However, timing of demographic expansion precedes the LGM in most of these species. Four species are fragmented phylogeographically within the region. Our results indicate that (i) demographic instability in response to historical climate change has been widespread in the Patagonian-Fueguian region, and is generally more pronounced at high latitudes in both southern and northern continents; (ii) colonization from lower latitudes is an important component of current Patagonian-Fueguian diversity; but (iii) *in situ* differentiation has also contributed to species diversity.

Keywords: biogeography, mammals, Patagonia, phylogeography, population genetics, Tierra del Fuego

Received 10 February 2010; revision received 6 May 2010; accepted 11 May 2010

Patagonia, poor as she is in some respects, can, however, boast a greater stock of small rodents than, perhaps, any other country in the World.

Charles Darwin, Diary, April 1834, Santa Cruz, Argentina

Introduction

Understanding current biotic diversity requires knowledge about how species have responded to long-term climate change, particularly through the glacial cycles of the Quaternary. Colonization from ice-free refugia

following the retreat of glacial masses is thought to have been an important component of the current composition of high latitude species diversity in the northern hemisphere (Hewitt 2000, 2004). Multiple refugia, both south and north of glacial ice sheets, are postulated to have preserved or fostered biological diversity during the Pleistocene (Rowe *et al.* 2004; Waltari *et al.* 2007), and genetic footprints of presumably postglacial colonization have been documented (Lessa *et al.* 2003; Runck & Cook 2005; Kotlik *et al.* 2006). Comparative analyses of western North America and western Amazonia showed a striking contrast: the former shows, as expected, genetic footprints of demographic expansion in many high latitude taxa (a signal that generally increases with latitude), whereas western Amazonia seems to have remained much more stable (Lessa

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et al. 2003). An extension of these types of comparisons, which requires intraspecific data from multiple species, to non-tropical areas of South America was not possible due to limited study cases. More generally, the role of glacial cycles in generating biotic refugia in non-tropical areas of the southern hemisphere has received relatively little attention (Beheregaray 2008).

Excluding Antarctica, South America is the only southern continent that extends significantly beyond 40 ºS. Large ice sheets centred on the southern Andes developed during glacial times (Rabassa 2008) and when combined with the narrowing of the southern cone, suggest a simple biogeographical scenario, alternating episodes of glacial expansion that forced the northward retraction of biota with episodes of southward colonization. However, much of the current area of Argentinean Patagonia and northeastern Tierra del Fuego remained unglaciated through the Late Pleistocene (Clapperton 1993; Rabassa *et al.* 2000). Furthermore, the large continental shelf in the southern Atlantic was exposed during the last glacial maximum (LGM), far compensating the area covered by ice sheets along the Andes. In contrast to northern continents, in which the last glaciation was among the largest, the largest glaciation in South America took place *c.* 1 million years ago (Rabassa *et al.* 2000). Thus, the generality of a scenario of postglacial colonization from a single, presumably northern refugium needs to be established on the basis of a comparative analysis of multiple species. One implication of the single refugium north of Patagonia scenario is that the Patagonian region did not foster speciation in association to glacial cycles.

Recent studies of two rodent species, based on samples concentrated along the southern Andes (*Abrothrix olivaceus*; Smith *et al.* 2001; Rodríguez-Serrano *et al.* 2006; and *Oligoryzomys longicaudatus*: Palma *et al.* 2005; Belmar-Lucero *et al.* 2009), have suggested demographic expansion associated with predominantly southward postglacial colonization. In contrast, a study of three plant species of the Patagonian steppe (Jakob *et al.* 2009) uncovered demographic stability and substantial local structure. The differences in the geographical and environmental coverage of these studies make it impossible to offer an integrative scenario for the entire Patagonian-Fueguian region and associated biomes. Here, we examine the issue with DNA sequences of 14 species (of the 18 species reported) of sigmodontine rodents in the region, providing the first broad, multispecies coverage of the Patagonian-Fueguian region. Sampling covers all major biomes (Argentinean monte, Patagonian steppe, of which the southernmost fragment is often labelled as Patagonian grasslands, and temperate Valdivian and subpolar Magellanic forests), from northern Patagonia to Tierra del Fuego (~40–54°S), and from the Atlantic to

the Pacific, including areas both covered and not covered by ice during the LGM. The working hypothesis stemming from available studies on rodents is that the current distribution of each species is the result of a postglacial expansion from a single, more restricted source area. Our geographical and environmental coverage of the distribution of the species that have already been studied is far more extensive, including the Patagonian steppe and Tierra del Fuego, permitting reassessment of earlier conclusions. More generally, expanding the survey to multiple species allows us to address the relative importance of fragmentation and of postglacial colonization in the historical biogeography of Patagonian-Fueguian rodents.

Materials and methods

We sampled small mammals extensively throughout Patagonia and Tierra del Fuego (Fig. 1). Eight hundred and one base pairs of the 5′ end of the mitochondrial cytochrome *b* gene were obtained from the following species (sample sizes, including those obtained from Genbank): *Akodon iniscatus* ($n = 14$); *Calomys musculinus* ($n = 20$); *Graomys griseoflavus* ($n = 21$); *Eligmodontia morgani* ($n = 17$); *E. typus* ($n = 30$); *Loxodontomys micropus* ($n = 12$); *Phyllotis xanthopygus* ($n = 15$); *Oligoryzomys longicaudatus* ($n = 45$); *Reithrodon auritus* ($n = 14$); *Chelemys macronyx* ($n = 18$); *Abrothrix olivaceus* ($n = 72$); *Abrothrix longipilis* ($n = 21$); *Euneomys chinchilloides* ($n = 13$); *Geoxus valdivianus* ($n = 9$). Sequences were deposited in GenBank (Accession numbers HM167761–HM167930, as well as additional sequences obtained from GenBank; see Supporting Information).

The monophyly of nominal species was established by phylogenetic analysis in the framework of a large database for sigmodontines. Bayesian analyses were conducted with Mr. Bayes 3.1 (Ronquist & Huelsenbeck 2003) for each species separately; each analysis consisted of two independent runs, each with three heated and one cold Markov chains. The model used included six categories of base substitution, a gamma-distributed rate parameter, and a proportion of invariant sites; all model parameters were estimated in Mr. Bayes. Uniform-interval priors were assumed for all parameters except base composition and GTR parameters, which assumed a Dirichlet prior process. Runs were allowed to proceed for 2 million generations with trees sampled every 200 generations per chain. Convergence on a stable log-likelihood value was checked by plotting the log-likelihood values against generation time. The first 25% of the trees were discarded as burn-in; remaining trees were used to compute a 50% majority rule consensus tree and obtain posterior probability estimates for each clade (Supporting information).
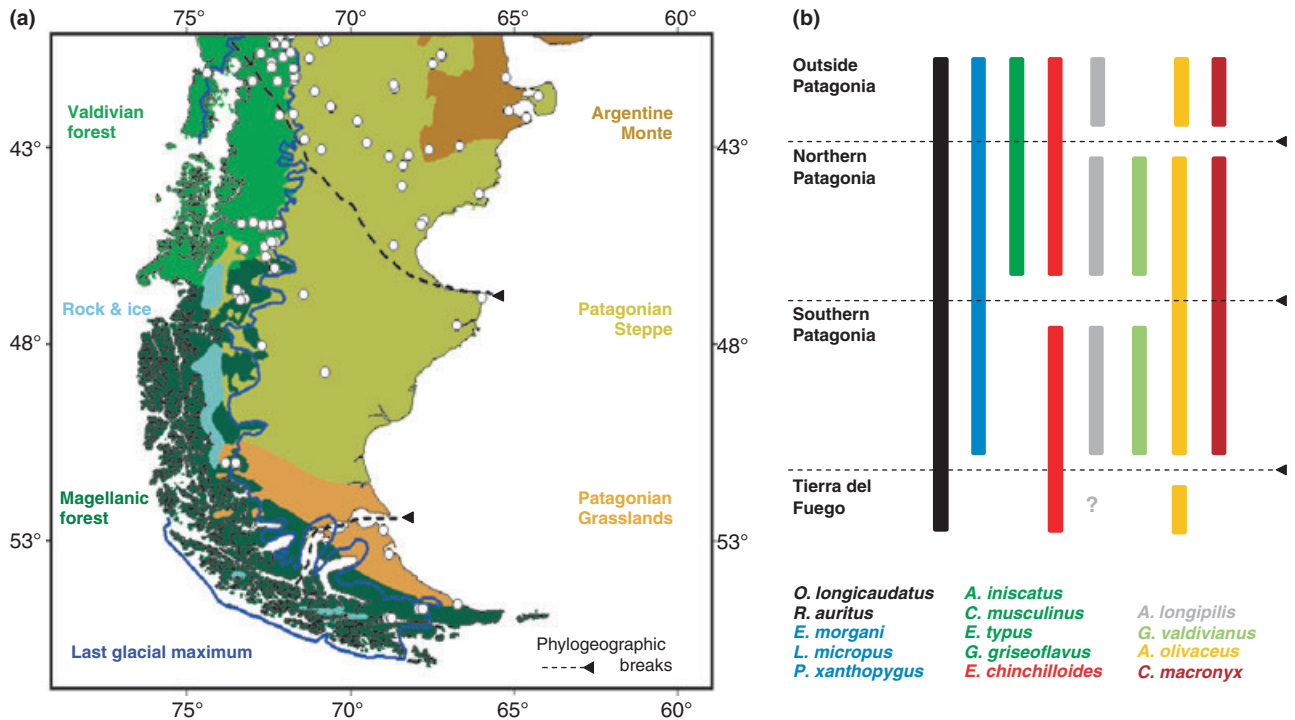
Fig. 1 (a) Map of southern South America indicating major biomes, sampled localities, approximate location of phylogeographic breaks identified in Patagonian-Fueguian rodents, and extent of the LGM (from Rabassa 2008). (b) Bar diagrams portray the phylogeographic units uncovered in Tierra del Fuego, Southern and Northern Patagonia and reference samples from areas outside the Patagonian-Fueguian region. The areas within the region are separated by dashed lines as in (a), but the samples outside Patagonia vary in location (details in Supporting Information).

Phylogeographic breaks were recognized as working hypotheses when accompanied by more than 3% divergence between them. Possible historical demographic expansion in each species or phylogeographic clade was assessed using maximum likelihood with Lamarc 2.1.3 (Kuhner 2006; Kuhner & Smith 2007), integrating results of three replicate runs, each consisting of 20 initial chains and 5 final chains, from which 2000 and 10 000 trees were sampled, respectively, using sampling increments of 20 generations, with the Felsenstein 84 mutation model. Fu's F_S test (Fu 1997) was used as a second assessment of demographic history using Arlequin 3.11 (Excoffier *et al.* 2005). Arlequin 3.11 was used to fit sudden expansion and spatial expansion models (Schneider & Excoffier 1999; Excoffier 2004) to estimate the relative timing of expansion. The significance of F_S, as well as the 95% confidence intervals on estimates of times of expansion, were established in Arlequin 3.11 on the basis of 1000 replicates. Relative time estimates were converted to absolute time using species-specific mutation rates (μ) obtained from calibrations of local relaxed clocks using Beast 1.4.8 (Drummond *et al.* 2006; Drummond & Rambaut 2007) and four calibration points from the fossil record (Pardiñas *et al.* 2002), with a dataset of 137

sequences that contained 2–4 representatives of the species of interest, plus one of each available species of the genus to which the target species belongs, one representative of the remaining sigmodontine genera, and one of each of the other subfamilies of Cricetidae that were used as outgroups. Results of five replicate runs, each consisting of 8 million generations sampled every 5000 generations under the GTR + I + G model, were combined after having discarded trees sampled before reaching the convergence zone. Posterior estimates of average rate of evolution of each species of interest were obtained from Beast using a routine kindly developed by Michael Defoin-Plate at our request: if a particular clade c, containing l external nodes, is found in a given tree sampled by Beast, then its average $r^{(B_c)} = \sum_{j \in B_c} r_j t_j / \sum_{j \in B_c} t_j$, where B_c is the set of the $2l - 2$ branches of c, t_j the amount of time that a branch j represents and r_j the rate of evolution along that branch. Thus the posterior estimate of the average rate of c is $E(r^{(B_c)}|D)$.

Results and discussion

Ten of the 14 species examined failed to show significant phylogeographic breaks within the Patagonian/

Fueguian region (Table 1). These single-clade species include those distributed in the study area mainly in central and northern Patagonia (*Akodon iniscatus, Calomys musculinus, Eligmodontia typus* and *Graomys griseoflavus*), as well as species that extend to the southern end of the continent (*Eligmodontia morgani, Loxondontomys micropus, Phyllotys xanthopygus,* and *Chelemys macronyx*) or, in the cases of *Reithrodon auritus* and *Oligoryzomys longicaudatus*, to Tierra del Fuego.

Four species, however, showed unanticipated geographic structure of genetic variation, consisting of more than one well-differentiated phylogeographic unit within the Patagonian-Fueguian region (Fig. 1). Among them, *Abrothrix longipilis* consists of two parapatric clades within the study area that differed by more than 4% observed sequence divergence; an additional reference sample of this species from north of Patagonia

Table 1 Tests of demographic expansion in Patagonian-Fueguian rodents

Taxon/unit	F_S	P	g
Single clade in Patagonia – Tierra del Fuego			
Akodon iniscatus[a]	−0.298	n.s.	367
Calomys musculinus[a]	−3.953	0.014	81
Graomys griseoflavus[a]	−8.026	0.001	1528**
Eligmodontia morgani[b]	−3.100	n.s	435
Eligmodontia typus[b]	−18.185	0.001	1197**
Loxodontomys micropus[b]	−2.048	n.s.	361
Phyllotis xanthopygus[b]	−8.208	0.001	535**
Chelemys macronyx[b]	−5.021	0.011	685*
Oligoryzomys longicaudatus[c]	−24.143	0.001	332**
Reithrodon auritus[c]	−5.984	0.005	399**
More than one clade in Patagonia – Tierra del Fuego			
Geoxus valdivianus[b]			
n Patagonia	−0.064	n.s.	26
Abrothrix olivaceus[c]			
Continental Patagonia	−24.849	0.001	866**
Tierra del Fuego	−1.946	n.s.	3006*
Abrothrix longipilis[c]			
n Patagonia	−1.993	n.s.	264
s Patagonia	−2.209	n.s.	1173**
Euneomys chinchilloides[c]			
n Patagonia	1.593	n.s.	260
s Patagonia	0.768	n.s.	43

Fu's F_S (Fu 1997) and corresponding significance level based on 1000 bootstrap replicates (n.s.: not significant at the 0.05 level) are provided. Estimates of g, the exponential growth parameter, are provided (*95% CI in the positive value range; **99% CI in the positive value range). Sample size was insufficient to examine the demographic history of the southern Patagonian clade of *Geoxus valdivianus*.
Species distributions in the region: (a) northern Patagonia; (b) continental Patagonia, (c) continental Patagonia and Tierra del Fuego.

(Province of Mendoza, Argentina) represents a third divergent clade. In line with earlier results (Smith *et al.* 2001; Rodríguez-Serrano *et al.* 2006), all Patagonian *Abrothrix olivaceus* belong to a single shallow clade; our results extend the known distribution of that clade substantially, especially to the south and on the Patagonian steppe. Unexpectedly, representatives of this species from Tierra del Fuego formed a distinct allopatric clade that differed from the continental unit by more than 4% observed sequence divergence. The two clades found in Patagonia and Tierra del Fuego are at least as divergent from each other as either one is from the northern Chilean clade reported by Smith *et al.* (2001), as well as from reference samples of *A. olivaceus* from the Province of Mendoza, Argentina, and samples from northern Chile (reported by Rodríguez-Serrano *et al.* 2006). Apparently, the continental and island clades of this species are separated by the Magellanic Strait. Regardless, this strongly suggests a history of fragmentation and differentiation within the Patagonian-Fueguian region.

Phylogeographic breaks found in the other three species occur within the continent (Fig. 1). *Euneomys chinchilloides* presents two clades that differ by more than 3% observed sequence divergence: one in Tierra del Fuego and southern Patagonia (Santa Cruz), and the other comprising samples from central and northern Patagonia and Mendoza. Finally, *Geoxus valdivianus* shows two distinct clades, in northern and southern continental Patagonia, which are not sister to each other and that differ by more than 10%, raising the possibility that they represent different species.

Another striking observed pattern is that phylogeographic breaks separate the various clades latitudinally, not by macrohabitat. In Patagonia, macrohabitats are roughly arranged west to east (Valdivian and Magellanic forests along the Andes, and open steppe and grasslands on the Atlantic slopes) with an intrusion of monte in NE Patagonia.

Three out of four species of Abrotrichini (a tribe of sigmodontines whose species diversity is centered on the southern Andes; D'Elía *et al.* 2007), but only one out of 10 non-abrotrichine species, show phylogeographic structure. A concentration of phylogeographic breaks among abrotrichines likely reflects a long history of association of this group to southern South America (Reig 1987), including the Patagonian-Fueguian region, and strongly suggests a history of differentiation that may have occurred, at least in part, within the region. Other studies in the Patagonian region have uncovered geographical structure suggesting local differentiation as well (Avila *et al.* 2008; Himes *et al.* 2008; Zemlak *et al.* 2008; Jakob *et al.* 2009).

Maximum likelihood estimations of g, the exponential demographic growth parameter were positive and

associated with 95 and 99% confidence intervals (CIs) in the positive range in nine out of 17 Patagonian-Fueguian main clades analysed; results of F_S tests are negative and significant in most of these cases, as well as in one additional species (Table 1). These potential cases of demographic expansion show a concentration among species that are represented by a single clade in Patagonia, but are not restricted to them.

Estimates of the relative timing of expansion of these clades based on a sudden expansion model, calibrated with evolutionary rates obtained with a relaxed molecular clocks, are accompanied with large CIs; however, although these estimates cover a broad range, several 95% CIs do not overlap (Fig. 2a). All 95% CIs of estimated times of demographic expansion fall within the last 500 000 years (Late Quaternary) and generally exceed 21 000 years (i.e. appear to be older than the LGM). Analyses using a spatial expansion model generally result in broader 95% CIs; still, only one of 10 cases

examined have CIs that include ages more recent than the LGM (Fig. 2b).

With some overlap, three classes of estimates of expansion times are suggested by the data: values for *Abrothrix olivaceus* from Tierra del Fuego and three additional species restricted to the mainland (*Calomys musculinus*, *Graomys griseoflavus*, and *Phyllotis xanthopygus*) are centred on the last 100 000 years; *Abrothrix longipilis* from southern Patagonia, *Oligoryzomys longicaudatus*, *Eligmodontia typus*, and continental *Abrothrix olivaceus* are centred on the 100 000–200 000 year range, whereas the CIs of *Reithrodon auritus* largely exceeds the latter value.

Historical demographic expansion is a prediction of a simple model that posits that much of the current fauna of a high-latitude region, such as Patagonia, has resulted from postglacial colonization from lower latitudes. Consequently, evidence of demographic expansion is often taken as indicative of a history of presumably postglacial colonization (Lessa *et al.* 2003; Hickerson & Cunningham 2005; Runck & Cook 2005). In many cases, unknown mutation rates preclude estimation of time of expansion, but assuming that the expansions detected using population genetic approaches must correspond to climate amelioration after the LGM may be unwarranted (Carnaval & Bates 2007). Studies of Patagonian fishes (Zemlak *et al.* 2008) and of a freshwater crab (Xu *et al.* 2009) have suggested earlier times of demographic expansion, but still within the Late Pleistocene.

Our results are consistent with a history of expansion subsequent to the LGM in one or a few species of Patagonian mice, but point to possibly older dates (up to 500 000 years or so) in most of the others (Fig. 2), with the following caveats. First, single locus estimates carry broad confidence intervals (Fig. 2), so it is hard to pinpoint precise dates and tie them to particular geological events. Second, the models used are relatively simple; more complex historical models might be needed to examine demographic change in geographically structured populations (Jesus *et al.* 2006). Finally, analyses assume strict neutrality, but is has long been recognized that certain types of selection can result in patterns of within-species variation similar to demographic expansion (Tajima 1989). However, the pattern is not limited to one or a few species, which argues in favour of a demographic explanation based on common history (Lessa *et al.* 2003).

Our results provide strong support for a model of demographic expansion from single, restricted source populations (Smith *et al.* 2001), with two noteworthy departures from expectations based on postglacial expansions from a single refugium. First, in agreement with a recent study of three plant species of the region
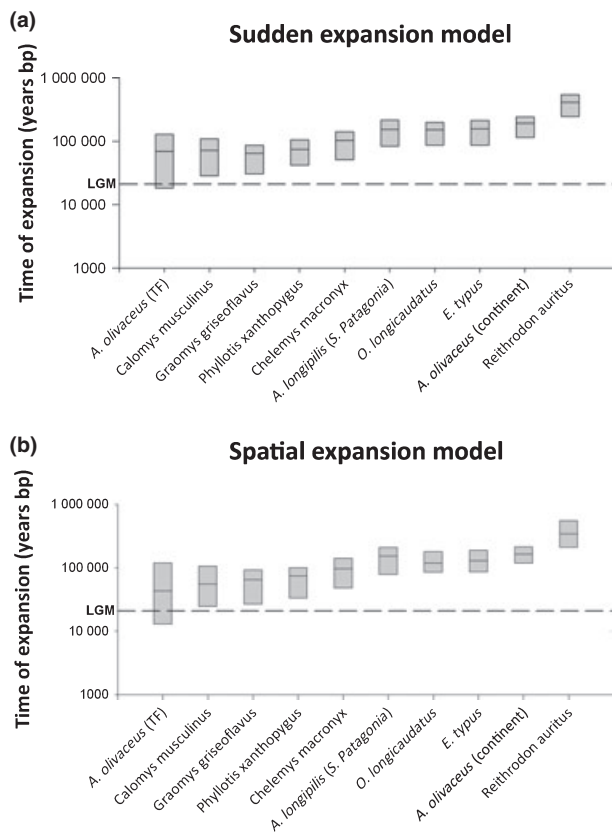
Fig. 2 Estimated times of demographic expansion of selected sigmodontine rodents of the Patagonian-Fueguian region. (a) 95% CIs of the time of demographic expansion (τ) obtained from a sudden expansion model. (b) Corresponding values obtained from a spatial expansion model. In both cases, the horizontal dashed line corresponds to the LGM, *c.* 21,000 years before the present.

(Jakob *et al.* 2009), four species of rodents show evidence of strong phylogeographic structure within the Patagonian-Fueguian region, as well as evidence of differentiation from references samples north of the study area (particularly Mendoza and Central Chile). Second, when demographic expansion is detected, it may be reasonably assigned to a period subsequent to the LGM only in a small fraction of species.

More generally, the latitudinal organization of phylogeographical breaks (in contrast with the east to west organization of macrohabitats), the presence of a distinct phylogeographical unit in Tierra del Fuego, and a history of local differentiation within Patagonia in some species emerge as significant findings that require further testing and refinement with larger samples and additional loci. The fact that many species have a history of demographic expansion, in contrast, is unlikely to change substantially with additional data. However, the timing of such demographic events and the location of source populations will be refined by future detailed studies.

In sum, the emerging pattern for the recent biogeographical history of Patagonia and Tierra del Fuego includes both recent (although possibly not always post LGM) colonization from lower latitudes, as well as differentiation within the region, particularly in the Abrotrichini, a tribe of mice centred on southern South America. Species and populations at high latitudes appear to be more susceptible to climate change, both in the short term (Montes-Hugo *et al.* 2009) and in association with historical climate cycles of the Neogene (Hewitt 2000; Lessa *et al.* 2003).

In conjunction with other studies of within-species genetic variation across the latitudinal gradient of biotic diversity, these findings indicate that: (i) demographic instability in response to historical climate change is more pronounced at high latitudes; (ii) colonization from lower latitudes is an important component of current diversity at high latitudes; and (iii) local processes, including within-region differentiation, deserve greater recognition.

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Supporting information

Additional supporting information may be found in the online version of this article.

Data S1 Lessa EP, D'Elía G, Pardiñas UFJ (2010). Genetic footprints of late Quaternary climate change in the diversity of Patagonian-Fueguian rodents. Molecular Ecology.

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