



## The evolutionary history of sigmodontine rodents in Patagonia and Tierra del Fuego

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*Received 1 March 2011; accepted for publication 1 March 2011*

The Patagonian and Fuegian regions host a rich assemblage of sigmodontine rodents. In this article, we present a synthesis of our current understanding of their late Neogene diversification. Sigmodontine diversity in this area encompasses 16 genera and about 24 species; however, most belong to the tribes Abrotrichini and Phyllotini. Several abrotrichine genera are endemic to the region, whereas phyllotines are represented mainly by species widely distributed outside Patagonia. Two main ecogeographical assemblages of sigmodontines can be recognized: a lowland northeastern group with species mostly associated with shrub formations of the Monte Desert, and a medium to highland southwestern group of typical Patagonian elements, including several abrotrichines and a diversity of Andean forms. The pattern of latitudinal decline in species' number in sigmodontine rodents is more complex than the traditionally envisioned north to south pauperization; southern mainland Patagonia is as poor in species' number as is northern Tierra del Fuego (six species), suggesting that insularity is insufficient to explain the island assemblage. Glacial cycles may have had a major role in the control of sigmodontine richness. The fossil Fuego–Patagonian sigmodontine record is restricted to late Pleistocene–Holocene times. Remarkable events include regional extinctions of several widespread southwestern species during the latest Holocene and a reworking of micromammal assemblages, probably as a result of anthropogenic environmental changes. Two main phylogeographical patterns can be broadly associated with the northeastern and southwestern groups. The northeastern assemblage basically comprises species without phylogeographical structure, whereas the southwestern group involves several lineages with deep phylogeographical breaks. The current Fuego–Patagonian sigmodontine assemblage is mainly composed of species that colonized the area from lower latitudes and by others that have differentiated *in situ*. © 2011 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2011, **103**, 495–513.

**ADDITIONAL KEYWORDS:** Argentina – Cricetidae – extinctions – phylogeography – Quaternary – refugia – Sigmodontinae.

La región Patagónico-Fueguina comporta un rico ensamble de roedores sigmodontinos. En este trabajo presentamos una síntesis del conocimiento sobre los procesos de diversificación del grupo durante el Neógeno tardío. La diversidad de sigmodontinos comprende 16 géneros y cerca de 24 especies; sin embargo, la mayor parte de las mismas pertenecen a las tribus Abrotrichini y Phyllotini. Varios géneros de abrotrichinos son endémicos de la región, mientras que los filotinos están en general representados por especies de amplia distribución fuera de Patagonia. Se pueden reconocer dos grandes ensambles eco-geográficos de sigmodontinos: un grupo nor-oriental de tierras bajas, con especies mayoritariamente asociadas a las formaciones vegetales arbustivas del Monte, y otro

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sud-occidental de tierras de mediana a alta elevación, que agrupa típicos elementos patagónicos, incluyendo abrotriquinos y una diversidad de formas andinas. El patrón de disminución latitudinal en el número de especies de sigmodontinos es más complejo que aquel tradicionalmente supuesto de una pauperización norte a sur. La porción continental más austral de Patagonia es tan pobre en número de especies como la porción norte de Tierra del Fuego (seis especies) sugiriendo que la insularidad es insuficiente para explicar el ensamble isleño. Los ciclos glaciales podrían haber jugado un papel principal en el control de la riqueza específica de sigmodontinos y mamíferos en general. El registro fósil de sigmodontinos en Fuego-Patagonia está restringido al Pleistoceno tardío y Holoceno. Eventos destacables en esta historia incluyen extinciones regionales de especies sud-orientales de amplia distribución durante el Holoceno tardío y una reestructuración de las comunidades posiblemente debida a cambios ambientales de origen antrópico reciente. Dos patrones filogeográficos principales pueden ser gruesamente asociados con los grupos nor-oriental y sud-occidental previamente reseñados. Mientras que el ensamble nor-oriental comprende básicamente especies sin estructura filogeográfica, el sud-occidental involucra varios linajes que muestran profundos quiebres. La fauna de sigmodontinos de Fuego-Patagonia está conformada mayoritariamente por especies que colonizaron desde bajas latitudes y por otras diferenciadas *in situ*.

**PALABRAS CLAVE:** Argentina – Cricetidae – Extinciones – Filogeografía – Cuaternario – Refugios – Sigmodontinae.

## INTRODUCTION

Relative to its surface area and latitudinal placement, the Patagonian–Fuegian region supports a high diversity of land mammals. From the Río Negro Province in the north to the Isla Grande de Tierra del Fuego in the southern tip (Tierra del Fuego, hereafter), about 80 species have been recorded (Table S1, see Supporting Information). More than 50% of them are rodents, and a single subfamily, the Sigmodontinae (Cricetidae), is represented by 16 genera and about 24 species. Interestingly, sigmodontine diversity is largely restricted to the tribes Abrotrichini and Phyllotini (two of at least nine tribes of Sigmodontinae), and the former has a substantial part of its diversity associated with the region.

The variety and abundance of Fuego–Patagonian field mice, as well as the poor representation of other extra-Patagonian speciose groups, such as marsupials and bats, have long been recognized in the literature (e.g. Darwin, 1839; Allen, 1905; Osgood, 1943; Pearson, 1983). The study of Fuego–Patagonian sigmodontine diversity and evolutionary history has increased in intensity in recent years, as documented below. However, there have been few efforts to provide a synthesis of our knowledge of the group in the region.

Sigmodontines have a long fossil record in South America, with the oldest remains aged at about 5 Ma (Prevosti & Pardiñas, 2009). In contrast, the more ancient Patagonian fossils are from late Pleistocene deposits (e.g. Pearson, 1987; Pardiñas & Teta, 2008), thus providing a very short time window to explore evolutionary processes. The knowledge of the Patagonian living assemblages is

uneven, positively biased towards the northwestern forest–steppe ecotone (the area around the city of San Carlos de Bariloche); in contrast, the central and austral tablelands are particularly under-represented in the literature (e.g. Pearson & Pearson, 1982; Monjeau *et al.*, 1998; Pardiñas *et al.*, 2003). Most of the taxonomic work on Patagonian field mice was produced between the end of the 19th and the first decade of the 20th centuries (cf. Osgood, 1943). Indeed, many genera that characterize Patagonia – *Chelemys*, *Euneomys*, *Loxodontomys*, *Reithrodon*, among others – are in need of systematic revision. Finally, until very recently, there were no more than a few phylogeographical studies of sigmodontine genera of the region (e.g. Hillyard *et al.*, 1997; Kim *et al.*, 1998).

During the last decade, several research efforts have produced rich data on the systematics and biogeography of Fuegian–Patagonian sigmodontine rodents (e.g. Smith, Kelt & Patton, 2001; Pardiñas *et al.*, 2008; Rodríguez-Serrano, Hernández & Palma, 2008; Teta, Udrizar Sauthier & Pardiñas, 2009; Feijoo *et al.*, 2010; Lessa, D’Elía & Pardiñas, 2010; Palma, Cancino & Rodríguez-Serrano, 2010). In the present contribution, we address three main topics: (1) the recent diversity and latitudinal pattern of pauperization; (2) fossil history; and (3) phylogeographical patterns. Our emphasis is on the Argentine drylands (39–56°S), but we also consider available data on adjacent Valdivian and Magellanic forests. The final goal of this review is to provide a baseline for the understanding of the evolution and historical biogeography of the sigmodontines in the southern portion of South America.

## THE RECENT SIGMODONTINE FAUNA

## SPECIES' COMPOSITION

Sigmodontine rodents in Fuego-Patagonia mostly comprise members of two tribes: abrotrichines and phyllotines (Table 1; Fig. 1).

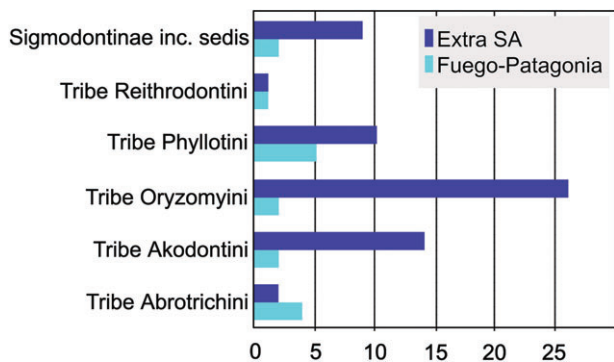
The Abrotrichini, a recently recognized tribe extirpated from the classical Akodontini, is a clade that encompasses four mostly Patagonian genera (*Notiomys*, *Geoxus*, *Chelemys* and *Pearsonomys*) of long-clawed fossorial and semi-fossorial forms, and related mice of the genus *Abrothrix* (e.g. Pearson, 1984; Patterson, 1992; D'Elía *et al.*, 2007). These five genera comprise nine species distributed along the southern Andes and neighbouring arid lands, and are adapted to environmental conditions ranging from the southern Andean forests to the Patagonian steppe. Although the genus *Pearsonomys* is endemic to the Pacific Valdivian forest (Patterson, 1992; D'Elía *et al.*, 2006b), *Abrothrix olivaceus* is one of the most widespread abrotrichines, reaching 56°S, the southernmost recorded sigmodontine. Abrotrichine genetic geographical structure also reinforces the concept of a long association history of this tribe with Patagonia (Lessa *et al.*, 2010, in press; see below).

Phyllotines show an important diversity in Patagonia, with six species belonging to five genera. During the last decade, successive molecular-based phylogenetic analyses (Smith & Patton, 1999; D'Elía, 2003; Steppan, Adkins & Anderson, 2004) have progressively reduced the number of species and genera recognized in this tribe. In contrast with the abrotrichines, phyllotine genera have substantial fractions of their distributions outside Patagonia (Table 1). Indeed, *Loxodontomys* is the only phyllotine genus that has most of its range in Patagonia. Remarkably, this tribe is today absent from Tierra del Fuego even though two of its genera, *Eligmodontia* and *Phyllotis*, reach the Magellan Strait. In general, phyllotines

seem to be more strictly related to arid and semi-arid environments (Hershkovitz, 1962; Mares, 1980), whereas abrotrichines are also associated with southern Andean forests.

*Euneomys* and *Reithrodon* are two very peculiar sigmodontines that were once considered to be members of the Phyllotini (Steppan, 1995), but have been shown to be distantly related to this tribe, as well as to each other (D'Elía, 2003; Steppan *et al.*, 2004). Both are medium to large in size, short tailed, densely furred, with hypsodont laminated molars, herbivorous in diet and nocturnal habits (Pearson, 1983, 1987, 1988). Data on their distribution and abundance along Fuego-Patagonia suggest some ecological differences between these rodents, with *Euneomys* dominating the harsh central and southwestern areas and *Reithrodon* occupying mainly oriental lowlands and northwestern steppes. The environmental preferences displayed by *Euneomys* might reflect an ancient connection to typical Patagonian habitats; fossil and genetic data strongly support this statement (see below). The long-tailed rat *Irenomys*, a unique sigmodontine genus restricted to the *Nothofagus* forest, is sister to *Euneomys*, according to molecular phylogenetic analysis (D'Elía *et al.*, 2006a). The morphological distinctiveness between them, however, seems to be indicative of a deep divergence and a long history of association (probably arising in the Pliocene) of *Irenomys* with southern forest environments.

Two additional sigmodontine tribes are represented in southern South America, Akodontini and Oryzomyini, the most diverse sigmodontine groups in the subcontinent (Musser & Carleton, 2005; Weksler, 2006). Interestingly, Fuego-Patagonian representatives of Akodontini and Oryzomyini are scarce (Fig. 1), in accordance with their preference for tropical-subtropical to temperate environments. The ubiquitous genus *Akodon* is the only akodontine genus reaching mainly the northeastern portion of Patagonia, where it is represented by the species *A. iniscatus* and *A. neocenus* (Pardiñas, 2009). Typical genera that live in temperate grasslands and have southern expressions, such as *Necomys* or *Oxymyzomys*, are not found beyond 39°S (Pardiñas *et al.*, 2004). Only one oryzomyine, the versatile hantavirus reservoir *Oligoryzomys longicaudatus*, is widely represented in Fuego-Patagonia (Palma *et al.*, 2005; Carbajo & Pardiñas, 2007). The low diversity of oryzomyines observed in Fuego-Patagonia also characterizes other nonforested environments, such as the Pampas and the Argentine Monte Desert.



**Figure 1.** Number of genera per tribe contrasting the Fuego-Patagonian region with the rest of South America (SA). Data from D'Elía *et al.* (2007).

## ASSEMBLAGES, DIVERSITY AND MAJOR BIOMES

Four main biotic units, mainly based on vegetation but also climate, topography and soils, are recognized

**Table 1.** The living sigmodontine rodent fauna of Fuego–Patagonia

Geographical distribution		Tierra del Fuego	Outside Patagonia	Main reference
Patagonia (mainland)				
<b>Tribe Abrotrichini</b>				
<i>Abrothrix hershkovitzi</i>	Not found	Cape Horn Is.	Not found	Patterson <i>et al.</i> (1984)
<i>Abrothrix lanosus</i>	Southwest Andean	Yes	Not found	Fejoo <i>et al.</i> (2010)
<i>Abrothrix longipilis</i>	Widespread except northeast portion	Yes	Reaching central Chile	Palma <i>et al.</i> (2010)
<i>Abrothrix olivaceus</i>	Widespread except northeast portion	Yes	Reaching north Chile	Osgood (1943)
<i>Abrothrix sanborni</i>	Central <i>Nothofagus</i> forest	Not found	Not found	Osgood (1943)
<i>Chelemys macronyx</i>	West Andean	Not found	Reaching central Chile	Osgood (1943)
<i>Geoxus valdivianus</i>	West Andean	Not found	Not found	Osgood (1943)
<i>Notiomys edwardsii</i>	West and central steppe	Not found	Not found	Pardiñas <i>et al.</i> (2008)
<i>Pearsonomys annectens</i>	Coastal central Chile	Not found	Not found	Patterson (1992)
<b>Tribe Akodontini</b>				
<i>Akodon azarae</i>	Northeast corner (marginal)	Not found	Widespread temperate grasslands	Pardiñas <i>et al.</i> (2003)
<i>Akodon iniscatus</i>	Northeast portion	Not found	Not found	Pardiñas (2009)
<i>Akodon necoenus</i> *	Northeast portion	Not found	Widespread semi-arid portion	Pardiñas (2009)
<b>Tribe Oryzomyini</b>				
<i>Holochilus brasiliensis</i>	Northeast corner (marginal)	Not found	Widespread northeast wetlands	Formoso, Sauthier & Pardiñas (2010)
<i>Oligoryzomys longicaudatus</i> †	Widespread	Yes	Reaching north Chile	Palma <i>et al.</i> (2005)
<b>Tribe Phyllotini</b>				
<i>Calomys musculus</i>	Widespread	Not found	Widespread semi-arid portion	Pardiñas <i>et al.</i> (2003)
<i>Eligmodontia morgani</i>	West and central steppe	Not found	Not found	Hillyard <i>et al.</i> (1997)
<i>Eligmodontia typus</i> ‡	Northeast portion	Not found	Widespread semi-arid portion	Hillyard <i>et al.</i> (1997)
<i>Graomys griseoflavus</i>	Northeast portion	Not found	Widespread semi-arid portion	Pardiñas <i>et al.</i> (2003)
<i>Loxodontomys micropus</i>	West Andean	Not found	Reaching central Chile	Cañon <i>et al.</i> (2010)
<i>Phyllotis xanthopygus</i>	Widespread except northeast portion	Not found	Not found	Osgood (1943)
<b>Tribe Reithrodontini</b>				
<i>Reithrodon auritus</i>	Widespread	Yes	widespread temperate grasslands	Osgood (1943)
<b>Sigmodontinae inc. sedis</b>				
<i>Euneomys chinchilloides</i> ‡	Widespread except northeast portion	Yes	Not found	Osgood (1943)
<i>Euneomys mordax</i>	Northwest Andean highlands	Not found	Not found	Pearson & Christie (1991)
<i>Irenomys tarsalis</i>	Central west forest	Not found	Not found	Pardiñas <i>et al.</i> (2004)

\*Including *A. molinae*.†Including *O. magellanicus*.

‡Ongoing studies suggest that these entities are composed of at least two species in Patagonia.

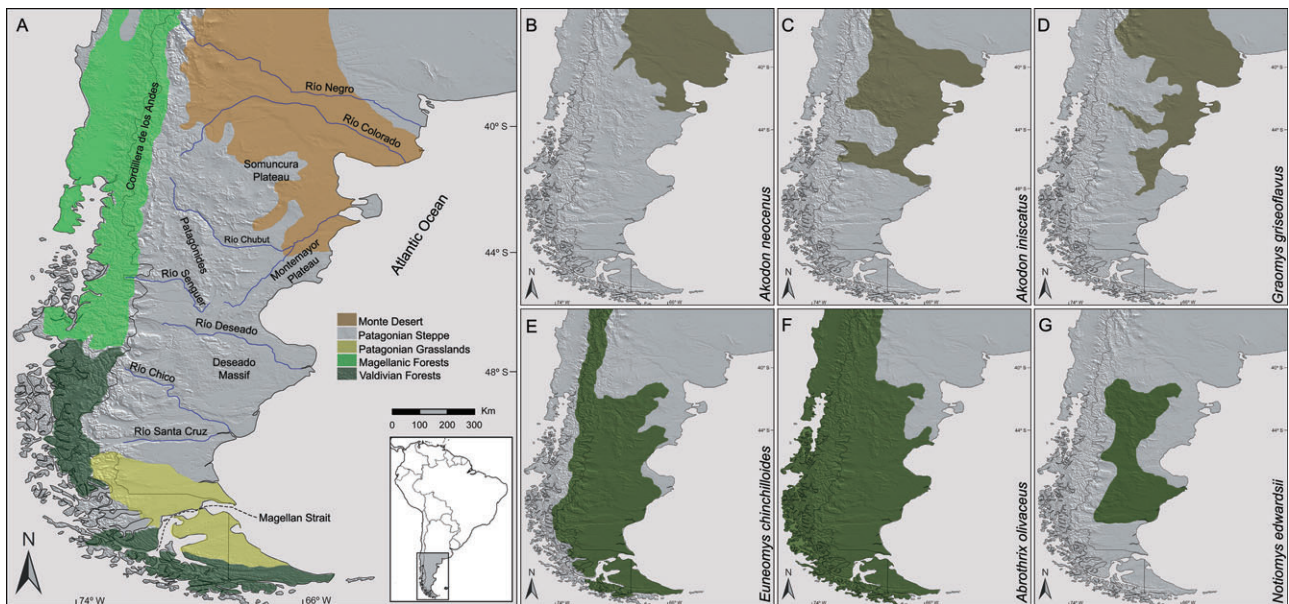
in Fuego–Patagonia (e.g. Soriano *et al.*, 1983; Coronato *et al.*, 2008; Fig. 2). Three are roughly arranged in a longitudinally oblique disposition from northeast to southwest: the Monte Desert, the Patagonian steppe (including a southern humid fragment distinguished as Patagonian grasslands) and the Magellanic tundra in the southernmost corner. A fourth unit, composed of the Valdivian and subpolar Magellanic forests, runs north to south as a narrow strip along the Andean foothills. The association of small mammal assemblages with these biotic units is not totally resolved (e.g. Osgood, 1943; Texera, 1973; Monjeau *et al.*, 1997, 1998; Pardiñas *et al.*, 2003; Trejo & Lambertucci, 2007), in part because of limited and uneven sampling efforts in the region. Fortunately, ongoing studies are providing new information about many poorly explored areas of Fuego–Patagonia (e.g. Pardiñas, Udrizar Sauthier & Teta, 2009; Udrizar Sauthier *et al.*, in press).

Sigmodontine rodents and other small mammals that inhabit Patagonian dry lands (including the Monte Desert and Patagonian steppe) can be divided into two main, partially overlapping, assemblages. The approximate geographical boundary between them runs along the West Central Patagonian hills ('Patagónides') to meet the Río Deseado valley and Deseado Massif (Fig. 2). One of these main assemblages is found in the northeastern Patagonian lowlands and comprises species typically linked to the Monte Desert, such as *A. neocenus*, *Calomys musculus* and *Graomys griseoflavus* (Figs 2, 3). This group is characterized by the predominance of akodontines

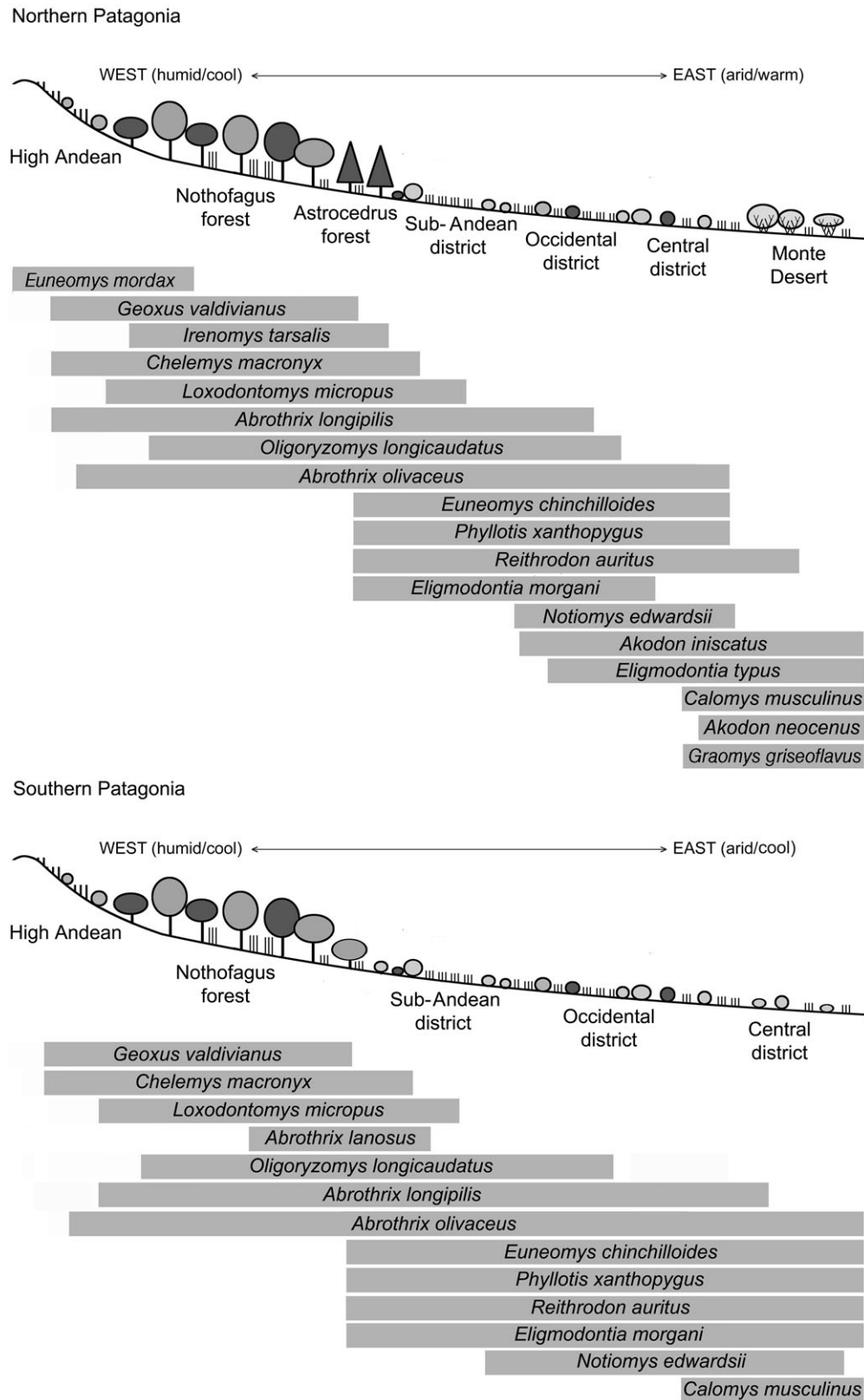
and phyllotines and the total absence of abrotrichines. Contrary to a general perception (Ojeda, Blendinger & Brandl, 2000), only some (e.g. *Akodon azarae*, *Holochilus brasiliensis*), but not all, members of this assemblage are 'marginal' in Patagonia. This misperception largely results from limited sampling, and the unappreciated fact that many typical Monte Desert taxa are found beyond the limits of this biome. For example, *C. musculus* and *G. griseoflavus* reach 48–50°S (Pardiñas *et al.*, 2003; Udrizar Sauthier *et al.*, in press), whereas the Monte Desert does not occur beyond 43°S (León *et al.*, 1998).

In contrast, a predominantly medium- to high-land assemblage, mostly comprising abrotrichines, some phyllotines (*Loxodontomys* and *Phyllotis xanthopygus*) and distinct sigmodontine lineages (such as *Euneomys*), dominates the rest of the Patagonian steppe and grasslands (Figs 2, 3). This group is more diverse than the northwestern group, includes several Patagonian endemics (e.g. *Notiomys*; Fig. 3) and shares species with the Valdivian and Magellanic forests (e.g. *Loxodontomys*, *Geoxus*) and the northern portion of Tierra del Fuego (Patagonian grassland biome).

Not all taxa strictly fit into this main division. For example, both *Oligoryzomys* and *Reithrodon* are widespread in Fuego–Patagonia, a distributional pattern that probably reflects recent dispersion events (see below). Moreover, important portions of central and coastal Patagonia display a complex altitudinal mosaic in which the two main rodent assemblages are present side by side. In these landscapes, largely



**Figure 2.** A, Map of Fuego–Patagonia showing the main geographical features and biomes mentioned in the text. B–G, The approximate distribution areas of some typical northeastern (B–D) and southwestern (E–G) sigmodontine rodents.



**Figure 3.** Distribution of sigmodontine rodent species along west–east gradients in northern (top) and southern (bottom) Patagonia.

allopatric species – such as the pairs *A. iniscatus* and *A. olivaceus*, or *Euneomys chinchilloides* and *G. griseoflavus* – are found in sympatry (but not syntopy). In addition, we are beginning to understand the fundamental role of river valleys as corridors. These landscape elements seem to have favoured dispersal, especially from east to west. The Río Chubut, the only Patagonian river studied in some detail in this context (Udrizar Sauthier, 2009), clearly shows a transitional westward dispersal of typical eastern faunistic elements.

These two main assemblages appear to have responded differently to geobiotic Neogene events. The northeastern group comprises species without phylogeographical structure in Fuego–Patagonia, whereas the southwestern group exhibits several phylogeographical breaks within the region (Lessa *et al.*, 2010, in press).

The Valdivian and Magellanic subpolar forests, associated with the Andean foothills, encompass a reduced assemblage of sigmodontine rodents (Fig. 3). Several are widespread forms, such as *A. longipilis* and *Loxodontomys micropus* (Pearson, 1983). Forest endemics include the genera *Irenomys*, an arboreal specialized rat, *Pearsonomys*, and the species *A. sanborni* (Osgood, 1943). Forest assemblages are still poorly known, particularly on the Argentine side. Apparently, some typical sigmodontines, such as *Irenomys*, are limited to forest environments north of the La Plata and Fontana lakes (45°S; Pardiñas *et al.*, 2004). South of this latitude, an endemic form of *Abrothrix*, *A. lanosus*, seems to be associated with a narrow strip of humid forest shrublands, reaching the southern coast of Tierra del Fuego (Feijoo *et al.*, 2010). The Magellanic tundra assemblage is even poorer than the Magellanic forests. Southernmost islands host *Abrothrix* species related to *A. olivaceus* from which putative endemic forms, such as *A. herskovitzi* or *A. llanoi*, are hard to distinguish; in addition, the widespread *Oligoryzomys* and *Euneomys* (cf. Osgood, 1943) are also present.

#### IMPOVERISHMENT PATTERN

Southern South America narrows as the latitude increases. As might be expected, a progressive pauperization of mammalian species is observed towards higher latitudes, a general pattern already recognized by several authors (e.g. Osgood, 1943; Texera, 1973). However, until very recently, distributional data were insufficient to examine this pattern in detail. The sigmodontine assemblages of Tierra del Fuego exemplify this point very well. Osgood (1943) recognized six sigmodontine species in the Archipelago, and highlighted differences in richness with respect to southern mainland populations. He also emphasized

insularity as an explanation for the reduced species' pool on the island, and pointed out the role of the Magellan Strait in enforcing isolation.

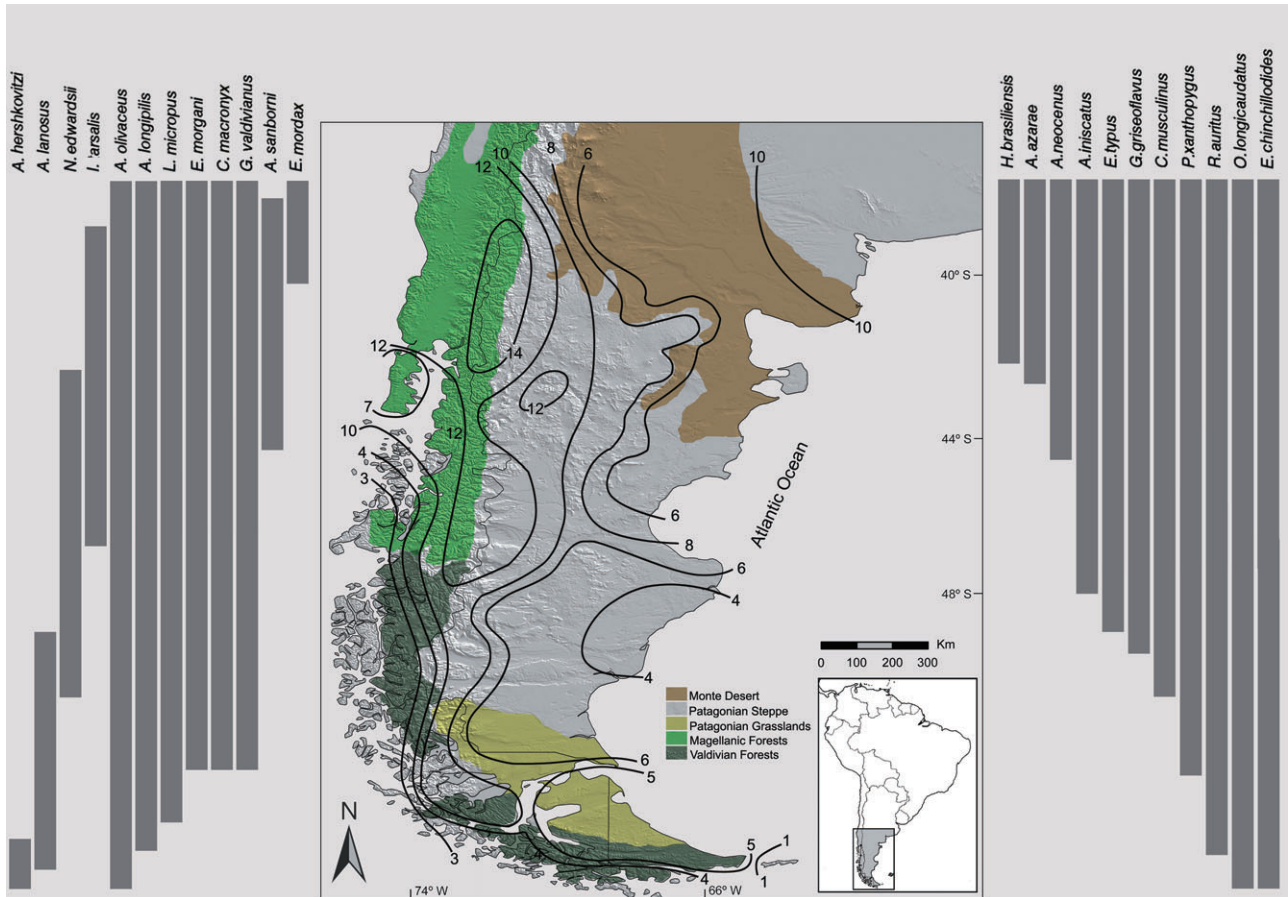
With substantially more data at hand, we provide the following outline of the pattern of sigmodontine diversity (Fig. 4): (1) the geographical pattern of species' number decay at higher latitudes is more complex than was previously envisioned; (2) several continental species disappear or are virtually absent before reaching the Magellan Strait; (3) the pattern differs between closed (Valdivian and Magellanic forests) and open (Monte, Steppe and Patagonian grasslands) biomes; and (4) very recent extinctions have occurred within the region.

The southernmost islands collectively support depauperized assemblages with no more than four species (Texera, 1973; Patterson, Gallardo & Freas, 1984). However, a very low species' number is also observed in the southern mainland, especially close to the Atlantic Ocean. For example, southern Santa Cruz steppe–grassland assemblages are as poor as those in northeastern Tierra del Fuego (six species in both cases). Moreover, several widespread Patagonian mainland species, such as *P. xanthopygus* and *Eligmodontia morgani*, have scattered populations associated with particular habitats in the vicinity of the Magellan Strait (Pardiñas *et al.*, 2009). Nevertheless, *Eligmodontia* might be present in suitable habitats of the northern portion of the island. This possibility is partially supported by its presence in the late Pleistocene archaeological assemblage of the Fuegian site Tres Arroyos 1 (U. F. J. Pardiñas, unpubl. data).

The most significant pauperization of Tierra del Fuego sigmodontine assemblages is mostly linked to forested environments. This can be illustrated by comparing records from Punta Arenas (a *Nothofagus* forest environment in the southern mainland) with those from the southern portion of Isla Grande de Tierra del Fuego. According to available data (cf. Osgood, 1943), the forest-dwelling genera *Chelemys*, *Geoxus* and *Loxodontomys* occur in the vicinity of Punta Arenas; in contrast, the dense forests of Isla Grande de Tierra del Fuego are exclusively occupied by *A. olivaceus*.

A significant decline in sigmodontine species' number seems to be associated with the Deseado Massif and the Río Deseado valley (Fig. 2), where several widespread species, such as *A. iniscatus* and *G. griseoflavus*, have their southernmost populations. A second break roughly coincides with the valley of the Río Santa Cruz, a southern distributional limit to sigmodontines such as *Notiomys*, as well as for other Patagonian mammals (e.g. the armadillo *Zaedyus*; cf. Allen, 1905).

The glacial history of the southern tip of South America may have contributed substantially to



**Figure 4.** Map of Fuego–Patagonia showing areas with similar numbers of species represented by black contours, superimposed onto major biomes. Grey vertical bars represent the approximate latitudinal ranges of sigmodontine rodents found in this region.

shape the sigmodontine diversity pattern at high latitudes. The forest areas of Tierra del Fuego were almost totally glaciated during the last glaciation and several earlier maxima (Rabassa, 2008). Thus, regional extinctions during glacial advances, coupled with variation in persistence and recolonization ability, might account for the observed distributional patterns. Genetic data (see below) suggest that *A. olivaceus* populations persisted during the last glaciation in a southern refugium, allowing the subsequent recolonization of Tierra del Fuego. Although the exact location of this proposed refugium is not clear, potential areas include northeastern Tierra del Fuego, which remained unglaciated through the most recent glaciations; other possible islands include Cape Horn and Isla de los Estados, or areas currently below sea level, especially on the eastern continental shelf.

Glacial advances – especially those of the early and middle Pleistocene – also deeply affected the southern mainland (Clapperton, 1993; Rabassa, 2008). It is

likely that, during deglaciation episodes, major rivers running towards the Atlantic Ocean probably played an important role as barriers for recolonization processes (Turner *et al.*, 2005). However, specific studies are needed to test this hypothesis. Faunal pauperization south of the Deseado Massif seems to be a product of glacial impact at these high-latitude extreme habitats.

## FOSSIL HISTORY

### LATE PLEISTOCENE DIVERSITY AND THE PLEISTOCENE–HOLOCENE TRANSITION

The oldest South American sigmodontine rodent fossils are found in sedimentary rocks of the Monte Hermoso Formation (*c.* 5 Ma, early Pliocene) in southeastern Buenos Aires Province, Argentina (Pardiñas, D'Elía & Ortiz, 2002; Prevosti & Pardiñas, 2009). These fossils are limited to a few fragmentary specimens, but show that several sigmodontine tribes were



present at that time in the continent, including Akodontini, Phyllotini and Reithrodontini (Reig, 1978; Pardiñas & Tonni, 1998). Fossil sigmodontine rodents are relatively frequent in Pliocene–Pleistocene deposits of the eastern Pampean region, including the first records in early–middle Pleistocene times of several of the extant species (Reig, 1978, 1986; Pardiñas, 1999a). In turn, no mammals that may be clearly linked to these latest Miocene–Pliocene or early Pleistocene records of the Pampean region have been found in Patagonia (Tonni & Carlini, 2008).

Late Pleistocene mammal remains are relatively abundant in Patagonia, especially in archaeological contexts representing the interval between 13 and 10 radiocarbon kiloyears ago ( $^{14}\text{C}$  ka) (Tonni & Carlini, 2008, and references cited therein). Although there are some small mammals associated with these sites, they are generally biased towards larger mammals.

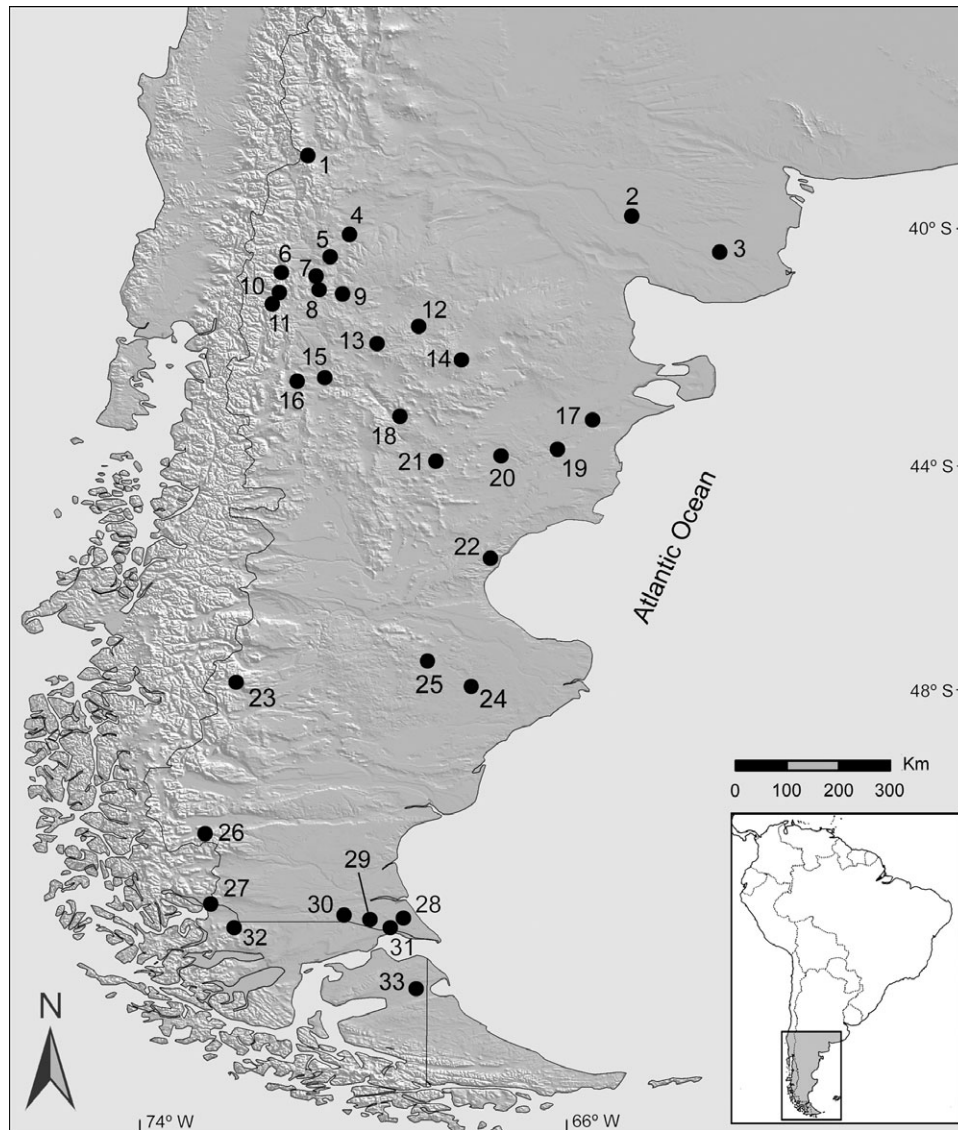
Sigmodontine samples for the time interval between 13 and 8  $^{14}\text{C}$  ka are represented by less than a dozen archaeological and palaeontological sites scattered throughout Fuego–Patagonia and collectively represent nearly all living species of the region (Pardiñas, 1999b; Figs 5, 6). At 10  $^{14}\text{C}$  ka, the El Trébol fossil samples in northwestern Patagonia are dominated by the presence of sigmodontines from open grassy areas and shrublands, such as *Reithrodon auritus* and *L. micropus*, respectively (Pardiñas & Teta, 2008). Between 10 and 8  $^{14}\text{C}$  ka, the assemblages of Cueva Trafal I and Cueva Epullán Grande are characterized by a lower species' number and the absence of primary *Nothofagus* forest sigmodontines, such as *Irenomys tarsalis* and *Geoxus valdivianus* (Pearson & Pearson, 1993; Pardiñas, 1999b; Pardiñas & Teta, 2008; Fig. 6). The only available sample from central Patagonia comes from a small cave of 12  $^{14}\text{C}$  ka that yielded an assemblage mostly dominated by typical sigmodontines from open shrubby and grassy areas, such as *Eligmodontia*, *A. olivaceus* and the rock-dweller *P. xanthopygus*. These data indicate a local landscape dominated by sparse shrubby vegetation mixed with bunchgrass patches and large rocky exposures (Teta *et al.*, 2009). In southern Patagonia, the assemblages recovered at Piedra Museo 1 (10.4  $^{14}\text{C}$  ka; Fig. 6) and Los Toldos (c. 9–8  $^{14}\text{C}$  ka) are consistent with a relative expansion of grassy steppes under cold and humid climatic conditions. Latest Pleistocene conditions in the southern tip of South America are represented by samples from Cueva del Milodón (13  $^{14}\text{C}$  ka) and the Fuegian site Tres Arroyos 1 (12  $^{14}\text{C}$  ka), both in Chile. Small mammal fossils from these assemblages are indicative of open areas under very cold and windy conditions with minor *Nothofagus* evidence in the mainland.

In summary, inhospitable and cooler conditions, with scarce vegetation cover and extensive open bare areas, may have been widespread across Patagonia during the late Pleistocene and most of the early Holocene, at the time of the first human arrival (Pardiñas & Teta, 2008; Teta *et al.*, 2009). In addition, it seems that, during the Pleistocene, areas of central Patagonia did not host species related to the Monte Desert (e.g. such as *A. iniscatus*, *C. musculus* and *G. griseoflavus*).

#### HOLOCENE STABILITY AND PROGRESSIVE COLONIZATION FROM THE NORTHEAST

Sequences covering the entire Holocene are scarce in Patagonia. In two classical archaeological sites of northwestern Patagonia, Cueva Trafal I and Cueva Epullán Grande (Fig. 6), Holocene samples suggest relative stability during the last 10  $^{14}\text{C}$  ka (Pearson & Pearson, 1993; Pardiñas, 1999b). Minor variations have occurred since the middle Holocene and indicate a progressive expansion of some northeastern forms towards the southwest, as well as brief expansions of mesic microenvironment-adapted species during cold and humid pulses (Pearson & Pearson, 1993; Pardiñas, 1999b). For example, in the Cueva Trafal I sequence, forest dwellers, such as *Geoxus valdivianus* and *I. tarsalis*, are well represented around 9.4–8  $^{14}\text{C}$  ka and 2.7–2.2  $^{14}\text{C}$  ka, respectively (Fig. 6), in agreement with the more humid conditions and expanded tree coverage suggested by palynological data for these periods (Heusser, 1993). Steppe vegetation in Cueva Trafal I is dominant, at least during the last 6.2 ky, possibly linked to a summer rainfall reduction between 8.5 and 5 ka (Markgraf, 1983); the earliest record of the arid land genus *Eligmodontia* is found in association with these changes (Fig. 6). Similar situations are also documented for the middle to late Holocene sequences of central Chubut (Udrizar Sauthier, 2009) and northwestern Santa Cruz (Pardiñas, 1998, 1999b). The middle Holocene was characterized by more humid conditions in northern Patagonia, contrasting with the northern Santa Cruz assemblages, which indicate a severe water deficit during the period between 7.5 and 4.7  $^{14}\text{C}$  ka (Pardiñas, 1999b).

Eastern forms, typically adapted to xeric shrub steppes of the Monte Desert, progressively expanded towards the west mostly during the middle to late Holocene. In northwestern Santa Cruz, the first appearance of *A. iniscatus* and *G. griseoflavus* is recorded around 7.6  $^{14}\text{C}$  ka, together with a frequency increase of *Eligmodontia* spp. (Fig. 6). In northwestern Patagonia, small mammal communities were enriched during the middle Holocene with the addi-

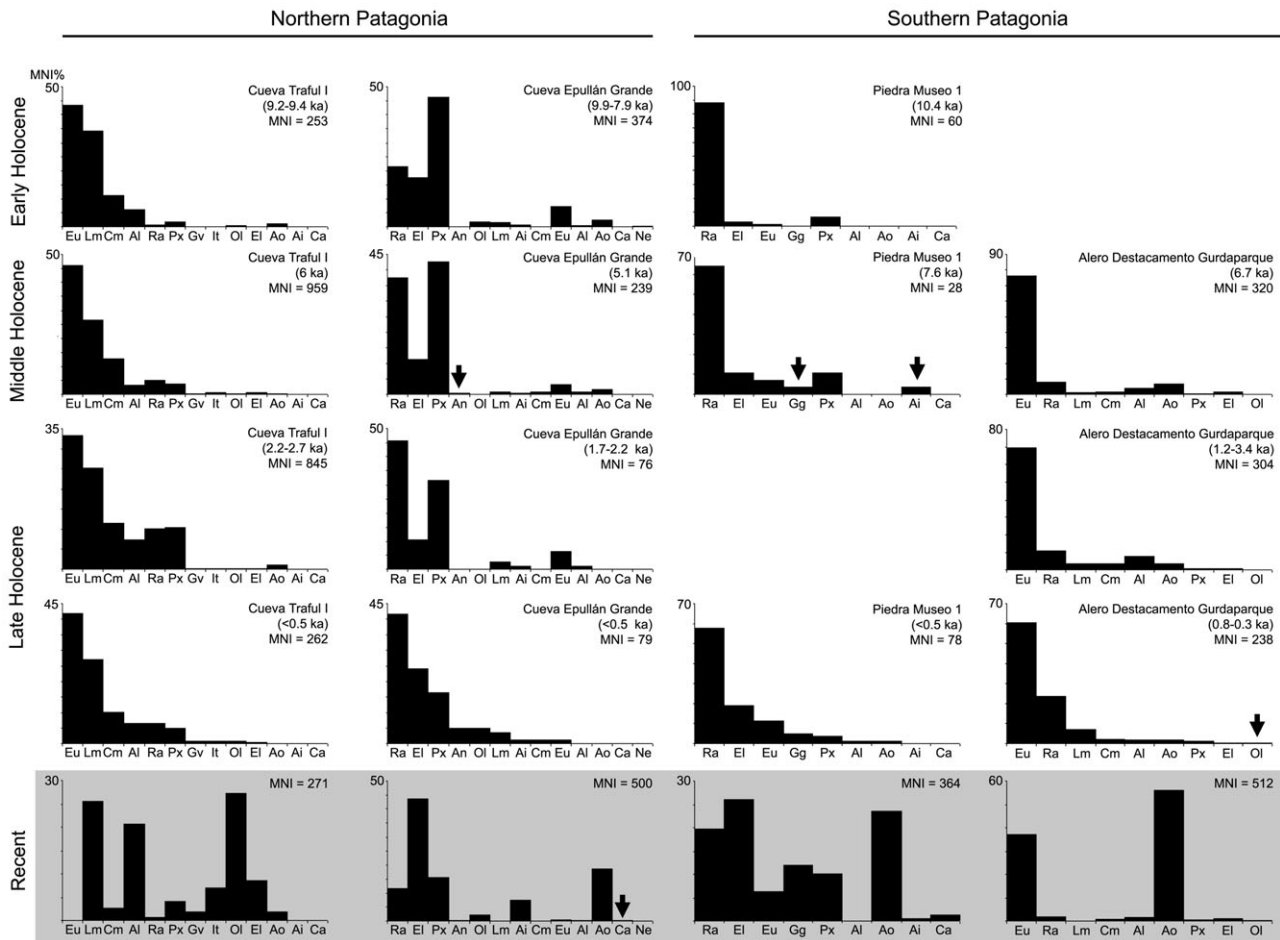


**Figure 5.** Main archaeological and palaeontological localities in Fuego–Patagonia: 1, Chenque Haichol [middle Holocene (MH) to late Holocene (LH)]; 2, Negro Muerto (LH); 3, Angostura 1 (LH); 4, Alero Arias (LH) and Rincón Chico 1 (LH); 5, Cueva Epullán Grande [early Holocene (EH) to LH]; 6, Cueva Trafal I (EH to LH); 7, Casa de Piedra de Ortega (LH); 8, Cuevas Sarita I, III and IV (LH); 9, Cueva and Paredón Loncomán (LH) and La Marcelina 1 (LH); 10, Estancia Nahuel Huapi (LH); 11, El Trébol [late Pleistocene (LP) to Holocene]; 12, Alero Santo Rosario (LH); 13, Cueva and Alero La Rural (LH); 14, Cueva Talagapa (LH); 15, Campo Cerdá I (LH) and Grieta Piedra Parada I (LH); 16, Cueva Watkins (LH); 17, Lle Cul (LH); 18, Grieta El Torito (LP); 19, Cueva de la Virgen (MH to LH) and Cueva Caolineria Dique Ameghino (LH); 20, Alero Las Plumas (LH); 21, Perfil Los Altares (LH); 22, Astra (LH); 23, Alero Destacamento Guardaparque (MH to LH) and Cerro Casa de Piedra 5 (MH to LH); 24, Piedra Museo 1 (LP to LH); 25, Los Toldos (EH); 26, Chorrillo Malo (MH to LH); 27, Dos Herraduras (LH); 28, Cerro Cóndor 1 (LH); 29, Bloque Puesto Pali Aike (LH); 30, Potrok Aike (LH); 31, Orejas de Burro 1 (LH); 32, Cueva del Milodón (LP to EH); 33, Tres Arroyos 1 (LP and LH).

tion of *A. neocenus* in Cueva Epullán Grande (Pardiñas, 1999b). Other expansive events occurred along the Río Chubut, involving *G. griseoflavus* and *Calomys* spp. (Udrizar Sauthier, 2009).

The late Holocene (after 3.5 ka BP) was a highly variable period in terms of climate, with a rich fossil

record that includes several extralimital occurrences for some sigmodontine rodents (Pardiñas, 1999b; Teta, Andrade & Pardiñas, 2005). Except for some sequences in northern or southernmost Patagonia, no unequivocal signals of climatic events of global occurrence, such as the Medieval Climatic Anomaly or the



**Figure 6.** Selected archaeological sequences of Fuego-Patagonia, showing changes in sigmodontine rodent abundance [expressed as a percentage of the minimum number of individuals (MNI) per period] through time; arrows indicate first occurrences of some taxa in the sequences. Abbreviations: *Akodon iniscatus* (Ai); *Akodon neocenus* (An); *Abrothrix longipilis* (Al); *Abrothrix olivaceus* (Ao); *Calomys* sp. (Ca); *Chelemys macronyx* (Cm); *Eligmodontia* spp. (El); *Euneomys* spp. (Eu); *Graomys griseoflavus* (Gg); *Geoxus valdivianus* (Gv); *Irenomys tarsalis* (It); *Loxodontomys micropus* (Lm); *Notiomys edwardsii* (Ne); *Oligoryzomys longicaudatus* (OI); *Phyllotis xanthopygus* (Px); *Reithrodon auritus* (Ra); ka BP, radiocarbon kiloyears before present.

Little Ice Age, have been detected (but also, see Rebane, 2002). Humid and cold pulses, in some cases related to glacier advances, presumably allowed the eastern expansion of some species, such as *L. micropus* and *Chelemys macronyx*, that are adapted to mesic microenvironments in the shrubby steppes of northern Patagonia (Teta *et al.*, 2005). Similarly, a cold and humid interval around 1.2–1 ka facilitated the ingress of *A. lanosus*, *Chelemys macronyx* and *L. micropus* into the eastern xeric steppes of the southern tip of the continent. In turn, warm and humid pulses, possibly associated with the Medieval Climatic Anomaly, might have allowed the range expansion of the amphibious rat *H. brasiliensis* along and across northern Patagonian streams (Fernández *et al.*, in press; Pardiñas & Teta, in press). The variety

of situations listed above suggests that, during the Holocene, northwestern Patagonian micromammal communities were the result of species-specific responses to environmental changes; massive replacements of species' pools across the west-east environmental gradient are not recorded.

#### RECENT EXTINCTIONS AND THE IMPACT OF HISTORICAL HUMAN ACTIVITIES

One main conclusion that emerges from the study of available fossils of sigmodontine rodents is that micromammal communities have remained relatively stable through most of the last 10 ky. In contrast, dramatic changes in assemblage composition have been recorded during the last century, involving deep

restructuring, local or regional extinctions and explosive increments of some opportunistic species. As there have been no significant climatic fluctuations during the last century, at least in comparison with those recorded during the Holocene, these changes must be mainly connected with human impact (Pardiñas, 1999b; Pardiñas *et al.*, 2000; Andrade & Teta, 2003; Teta *et al.*, 2005). Since the end of the 18th century, the massive introduction of sheep and, to a lesser extent, cattle occurred over nearly all of Patagonia, reaching a maximum in the 1940s and 1950s (Aagesen, 2000). Human impact also included shrub extraction and deforestation. Finally, in the lower valley of the Río Chubut, anthropogenic activities deeply modified the original environments, turning extensive natural areas into cultivated fields during the last 150 years (Pardiñas *et al.*, 2000; Udrizar Sauthier, 2009). In the entire region, these changes were coupled with fire regime alterations, desertification and the introduction of exotic species (e.g. Veblen *et al.*, 1999; Kitzberger & Veblen, 2003).

In central Patagonia, local extinctions included the disappearance of *A. longipilis*, *L. micropus*, *Notiomys edwardsii* and *O. longicaudatus* from the central portion of the Río Chubut valley (Udrizar Sauthier, 2009). *Loxodontomys micropus* also disappeared from the southern edge of the Somuncurá plateau (Andrade, 2009). In turn, opportunistic species, such as *Calomys* spp. and *O. longicaudatus*, took advantage of these changes, and their populations increased in size and geographical distribution. In some areas of the Río Chubut, *Calomys* accounts for up to 95% of the total small mammals recorded in owl pellets (Pardiñas *et al.*, 2000). In western grassy steppe areas, shrub expansion and grassland reduction produced by cattle overgrazing and the introduction of some exotic shrubs favoured increases of *A. olivaceus* and *Eligmodontia* spp. (see Pearson, 1983; Monjeau, 1989; Teta *et al.*, 2005), and probably allowed the expansion of *A. iniscatus* into northeastern Patagonia. However, not all local extinctions can be linked to human impact. For example, *H. brasiliensis* disappeared from northern Patagonia during the last few hundred years (< 400 years), perhaps in association with the Little Ice Age (Pardiñas & Teta, *in press*).

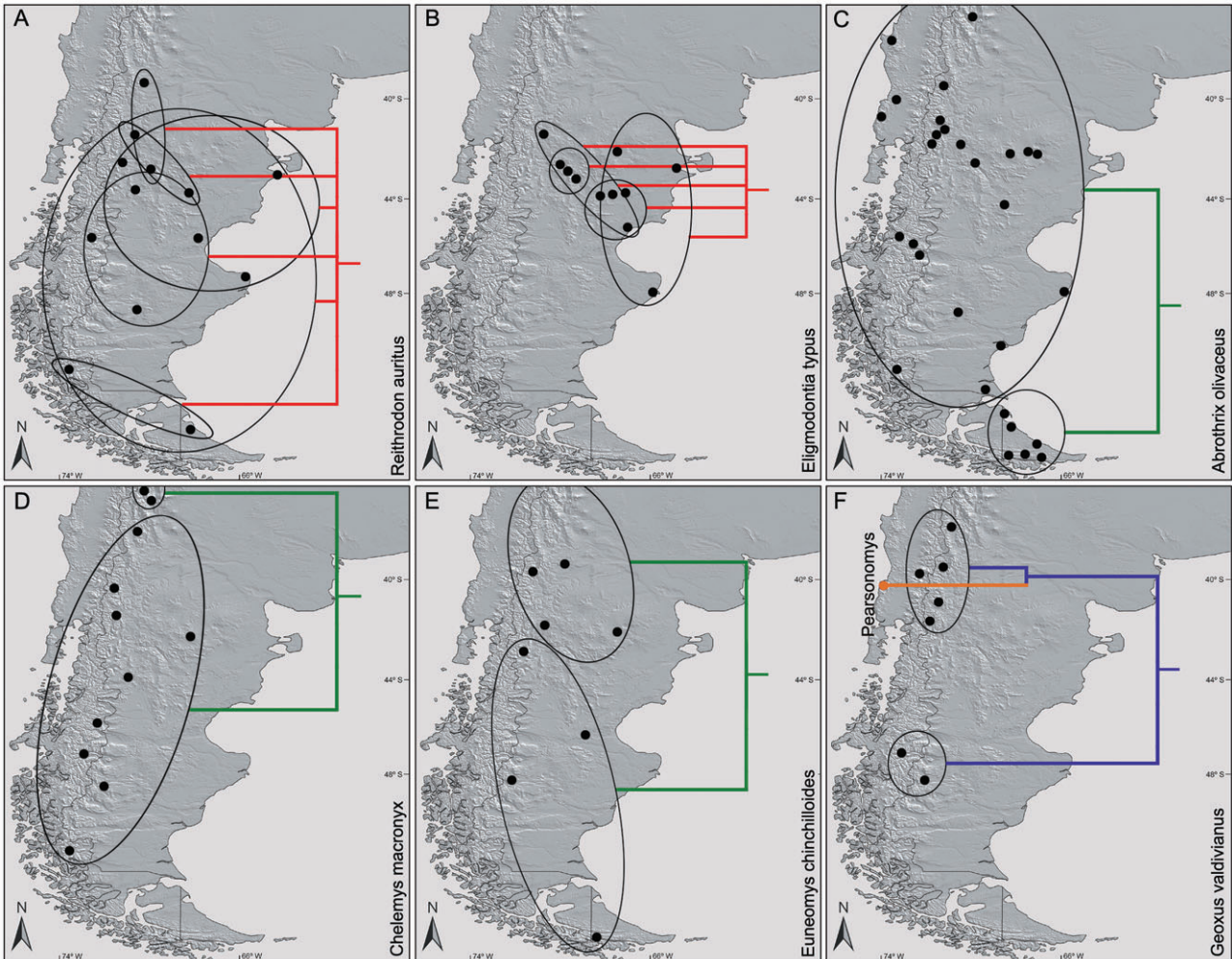
A less studied, but no less intriguing, phenomenon is the drastic decrease in abundance of *Euneomys* spp. in some areas of northwestern Patagonia after 10 000 or more years of predominance (Pearson, 1987; Pearson & Pearson, 1993; Pardiñas, 1999b; Fig. 6). Several hypotheses have been proposed to explain the causes of this event, including changes in fire regimes and the introduction of exotic pathogens (Pearson, 1987; Rebane, 2002). Introduced livestock may, however, be the most likely explanation for the

decline of *Euneomys*, through the replacement of bunchgrass with spiny shrubs (Rebane, 2002) and a drastic reduction in open areas (Veblen & Markgraf, 1988). Of course, this phenomenon did not occur uniformly across Patagonia, and *Euneomys* is still dominant in some open, hostile, rocky areas of central and southern Patagonia (Pardiñas, 1999b; Pardiñas *et al.*, 2003; Andrade, 2009).

## PHYLOGEOGRAPHICAL PATTERNS

Remarkably, although rodents have played a central role in studies on the effects of Quaternary glaciations on the biota, as in tropical South America (e.g. Lessa, Cook & Patton, 2003), Eurasia (e.g. Michaux, Libois & Filippucci, 2005), Africa (e.g. Nicolas *et al.*, 2006) and North America (e.g. Runck & Cook, 2005), few studies (Smith *et al.*, 2001; Cañón *et al.*, 2010; Lessa *et al.*, 2010) have been directed at addressing this issue in southern South America. More generally, few genetic-based studies have advanced hypotheses on the effect of Neogene glaciations on the sigmodontine fauna of southern South America. From the available information, it is clear that we are far from having a full understanding of the response of this group to historical climate change, although some generalizations may be advanced from the observed geographical patterns of genetic diversity.

Patagonian–Fuegian sigmodontines display three main phylogeographical patterns (Cañón *et al.*, 2010; Lessa *et al.*, 2010; Fig. 7). A set of species shows low levels of genetic variation and lacks phylogeographical structure. These single-clade species are those distributed mainly in central and northeastern Patagonia (*A. iniscatus*, *C. musculinus*, *Eligmodontia typus* and *G. griseoflavus*) and also include species extending to the southern end of the continent (*Eligmodontia morgani*) or to Tierra del Fuego (*R. auritus* and *O. longicaudatus*; see Belmar *et al.*, 2009). The second broad observed pattern is represented by six species that exhibit phylogeographical structure within the Patagonian–Fuegian region. Thus, *A. longipilis*, *A. olivaceus*, *Chelemys macronyx*, *E. chinchilloides*, *L. micropus* and *P. xanthopygus* show genetic variation that is geographically structured within the study area. All these species belong to the southwestern ecogeographical assemblage that characterizes the Fuego–Patagonian steppe and, in some cases, adjacent forested areas. The third pattern is exhibited solely by *Geoxus valdivianus*, a species that shows two distinct clades, one in northern and the other in southern continental Patagonia; these clades are not sister to each other and differ by more than 10%, raising the possibility that they may represent different species (Lessa *et al.*, 2010). The genetic data available thus far on *A. lanosus* (Feijoo *et al.*, 2010)



**Figure 7.** Examples of the three main phylogeographical patterns shown by Patagonian–Fuegian sigmodontine rodents. Pattern 1: *Reithrodon auritus* (A) and *Eligmodontia typus* (B) lack phylogeographical structure within the study region. Pattern 2: *Abrothrix olivaceus* (C), *Chelemys macronyx* (D) and *Euneomys chinchilloides* (E) have more than one allopatric clade; note that the location of the phylogeographical break differs among species. Pattern 3: *Geoxus valdivianus* (F) presents two geographically segregated clades that are not sister to each other; note that one of them is sister to *Pearsonomys* (orange line).

and *N. edwardsii* (Pardiñas *et al.*, 2008) are insufficient for inferences of their genetic structure.

Among the species of the second group, the observed divergence between clades varies from 2% (*Chelemys macronyx*; Alarcón *et al.*, in press) to around 5% (*A. longipilis*; Lessa *et al.*, 2010). Similarly, the number and distribution of phylogeographical units are also variable. *Abrothrix longipilis* is the most diverse species with three parapatric clades within the study area: (1) Tierra del Fuego and southern Patagonia; (2) central Patagonia; and (3) northern Neuquén in northern Patagonia (Lessa *et al.*, 2010; see also Palma *et al.*, 2010). The other species present two clades. Patagonian haplotypes of *A. olivaceus* belong to a single shallow clade (Smith *et al.*, 2001;

Rodríguez-Serrano, Cancino & Palma, 2006), and those from Fuegian specimens form a distinct clade (Lessa *et al.*, 2010). The phylogeographical breaks of *E. chinchilloides* and *L. micropus* are broadly congruent with that shown by *A. longipilis* at middle latitudes of Patagonia (Cañón *et al.*, 2010; Lessa *et al.*, 2010; see Figure 7 for examples of phylogeographical patterns).

It is noteworthy that the phylogeographical breaks separate the various clades latitudinally, rather than macrohabitat or segregating units east and west of the Andes (Lessa *et al.*, 2010; see also Himes, Gallardo & Kenagy, 2008; Patterson, 2010).

The existence of phylogeographical structure within the Patagonian–Fuegian region strongly suggests a

history of differentiation that may have occurred, at least in part, within the region (Lessa *et al.*, 2010). Similarly, other studies in the Patagonian region have uncovered geographical structure suggesting local differentiation as well (Avila, Morando & Sites, 2008; Zemplak *et al.*, 2008; Jakob, Martinez-Meyer & Blattner, 2009; Cosacov *et al.*, 2010). Further, for several sigmodontine species, genetic data provided no evidence of range shifts towards the north during the Last Glacial Maximum. The available data suggest the survival of large populations within their current distribution ranges, or at least within the region. In contrast, southward colonization, initially suggested by Smith *et al.* (2001), probably took place in species such as *G. griseoflavus*, as noted above. Although the exact number and location of glacial refugia remain unknown (Cañón *et al.*, 2010), it is clear that some of the refugia for at least some species must have been located at higher latitudes. In the case of *A. olivaceus*, this includes Tierra del Fuego.

Importantly, several phylogeographical units show signals of demographic expansion (Cañón *et al.*, 2010; Lessa *et al.*, 2010), which is often taken as indicative of a history of presumably postglacial colonization (Hewitt, 2000; Lessa *et al.*, 2003). However, mitochondrial DNA-based estimates of expansion times for these clades, using species-specific Bayesian estimates of mutation rates, fall within the last 500 000 years (late Quaternary) and generally are older than the Last Glacial Maximum (Lessa *et al.*, 2010).

In summary, the emerging pattern for the recent biogeographical history of sigmodontines in Patagonia and Tierra del Fuego includes both recent (although not necessarily post-Last Glacial Maximum) colonization from lower latitudes, as well as differentiation within the region. Multiple refugia, including some at higher latitudes, need to be invoked to explain the distribution of current genetic diversity harboured by sigmodontine populations (for a synthesis of this issue across diverse Patagonian taxa, see Sársic *et al.*, 2011).

#### THE EVOLUTION OF FUEGO–PATAGONIAN SIGMODONTINE ASSEMBLAGES: SUMMARY AND PROSPECTS

Our attempt to provide a comprehensive review of the history of sigmodontine rodents in Fuego–Patagonia has been made possible by significant advances in the study of current and historical distributions of these small mammals and their environments, coupled with taxonomic, phylogenetic and phylogeographical efforts. The data at hand are sufficient to indicate that: (1) the diversification of Fuego–Patagonian sigmodontines has involved both local differentiation

and colonization from northern sources over a time scale of at least one million years; (2) most demographic changes reflected by patterns of genetic variation trace back to the last 500 000 years, but few of these are likely to be post-glacial; (3) local extinctions, colonization and changes in abundance have occurred through the late Pleistocene and Holocene in association with climate change; and (4) similar classes of changes have occurred most recently, often as a result of human-related activities that have impacted local habitats.

There are limitations to these inferences related to insufficient and uneven coverage of the vast Fuego–Patagonian region in terms of both current diversity (including genetic data) and fossil and subfossil data, as well as a lack of comprehensive taxonomic studies of the taxa involved. These limitations, as well as others inherent to the data analysed, preclude a greater integration of fossil and molecular data.

Some apparent unconformities between fossil and genetic inferences of species' history serve to illustrate the limitations of the available data. For instance, the fossil record indicates that *C. musculinus* entered Patagonia in the last few thousand years, whereas genetic estimations suggest older times of expansion. The incompleteness of the fossil record may explain this incongruence. However, genetic inferences are based on simplified models and, at this point, a single locus, and should be interpreted with much caution.

It is clear that much more detailed work will be needed in order to refine the general outline provided here and to establish rigorous ties to geological events suffered by Fuego–Patagonia during the Neogene (Clapperton, 1993; Rabassa, 2008). The role of rivers and their changes during glacial cycles is not fully understood, but was possibly important both for dispersal and as potential barriers. Extensive flooding episodes also characterized the late Neogene history of the region and were large enough to produce extensive gravel beds – the famous 'Rodados Patagónicos' – from tablelands to the coast (Clapperton, 1993; Martínez & Kutschker, 2011). Geocryogenic processes, especially those that surely affected central plateaus during glacial advances, need to be studied in detail. However, the recorded wedge ice casts in northeastern Patagonia suggest that much of the nonglaciated territory was also under extremely harsh environmental conditions (Trombotto, 2008, and references cited therein). Recently published evidence on hyperarid conditions during several Pleistocene periods (Bouza *et al.*, 2007) adds a new piece to this complex puzzle. Finally, we still have very few data to adequately understand the potential role played by the Atlantic

Ocean continental shelf, which was largely exposed during glacial advances (Clapperton, 1993; Rabassa, 2008; Ponce *et al.*, 2011).

Genetic data on Fuego-Patagonian sigmodontine rodents have accumulated rapidly in recent years. Some patterns are beginning to emerge, but it is clear that multilocus data and substantially expanded geographical sampling are necessary to identify potential refugia and to distinguish them from recolonized areas, examine the relative importance of shared versus idiosyncratic species' responses to long-term climate change and to reduce the uncertainty associated with a single mitochondrial gene. The interplay between presumably neutral divergence associated with phases of geographical isolation and adaptive divergence in response to environmental variation is only beginning to be examined in Fuego-Patagonia (e.g. Ruzzante *et al.*, 2011).

Finally, the integration of sigmodontine results with those obtained for other components of the Fuego-Patagonian biota is of much need to gather a general picture that, for example, may identify the location of Pleistocene refugia. In this sense, a recent and intense surge of interest in the biogeography of southern South America (e.g. Ruzzante *et al.*, 2011; Sérsic *et al.*, 2011), which has developed among different research groups, beckons an era of profound learning of this unique and marvellous part of the world.

#### ACKNOWLEDGEMENTS

The authors are indebted to the organizers of the 2009 Workshop in La Plata, Argentina, J. Rabassa, D. Ruzzante, E. Tonni and A. Carlini, for the opportunity to present part of this contribution. This review was based on data that were obtained, processed or discussed with many students and assistants, including A. Formoso, D. Podestá, G. Cheli, D. Udrizar Sauthier, J. Sánchez, G. Mendos, G. Massaferró, J. Guzmán, C. Cañón, O. Alarcón, J. Martínez, A. Parada and C. Sierra. Access to archaeological samples was made possible by many archaeologists, especially L. Borrero, F. Martín, E. Crivelli-Montero, M. Fernández, L. Miotti, M. Massone, M. Salemme, E. Moreno, C. Belevi, R. Goñi, C. Aschero, J. Belardi, R. Barbarena, A. Sanguinetti de Bórmida, T. Civalero, J. Gómez Otero, M. Silveira and M. Boschín. Daniel Ruzzante, Mariana Morando and one anonymous reviewer made valuable suggestions in an earlier version of this work. Economic funds for field and laboratory activities were provided by Consejo Nacional de Investigaciones Científicas y Técnicas (PIP 6179) and Agencia (PICT 32405 and PICT 2008-0547) (to UFJP), Comisión Sectorial de Investigación Científica-Universidad de la República (PEDECIBA)

and The National Geographic Society (CRE 7813-05) (to EPL) and Fondo Nacional de Desarrollo Científico y Tecnológico (11070157 and 1110737) (to GD). Our deepest gratitude is expressed to these persons and institutions.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Table S1.** Living mammals recorded in southern Argentina and Chile (compiled from several sources).

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