



Patterns in community assemblage and species richness of small mammals across an altitudinal gradient in semi-arid Patagonia, Argentina



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ABSTRACT

This is the first study that explored the altitudinal gradient in Argentine Patagonia. The purpose of this study was to document the effects produced by altitudinal gradients in the arid lands on the community composition, abundance, and species richness of small mammals. Four hypotheses of factors that influence the patterns of diversity proposed for mountain regions were assessed for Patagonian arid lands: reduction in the effective area, changes in biotic and abiotic parameters, isolation of montane communities and feedback between zonal communities. The study was carried out in the Somuncurá Protected Natural Area (500–1600 m a.s.l.), a basaltic plateau from northern Extranorthern Patagonia. Mammals were sampled along altitudinal and vegetation gradients. With at least 20 small mammal species, Somuncurá is the place with the uppermost species richness in Patagonia. Small mammal abundance and species richness peaked at intermediate levels (750–1000 m a.s.l.), following a hump-shaped pattern. Temperature is the main factor to the structuring of small mammal communities in the arid lands and is the reason why height and latitude have a similar effect in the species composition. The same spatial pattern can be tracked throughout past climatic changes. Somuncurá should be considered at a higher priority level for conservation.

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1. Introduction

When a biogeographer has the opportunity to study an unexplored and isolated region, the first scientific purpose is as simple as inevitable: establish the baseline. Therefore, our first target was: 1) to survey a poorly known place, the Somuncurá plateau, in order to identify high biodiversity areas for small mammals in Patagonia. After this descriptive phase, our scientific objectives were: 2) to assess the influence produced by elevational gradients in the arid Patagonian plateaus on species richness and the species composition of small mammal assemblages, and 3) to explore the biogeographical affinities between the Somuncurá plateau and the major landscape units in Patagonia in order to contribute to conservation

programs for the arid lands. Moreover, some of the hypothesis proposed to explain the patterns of distribution of small mammals along altitudinal gradients were discussed in this study as possible explanations of the patterns observed.

Several studies on mountainsides have been conducted elsewhere. The environmental variables correlated with elevation generate and maintain the biogeographical patterns of species richness and biodiversity (Brown, 2001). The distribution and abundance of species along elevation gradients is often associated with variation in temperature and precipitation (Kelt, 1996; Kelt et al., 1994; Meserve et al., 1991; Patterson et al., 1990).

Different biotic response to elevation has been documented in previous works. For instance, a peak in species richness of small non-volant mammals at some intermediate altitude (via hump-shaped pattern, Li et al., 2003; Md Nor, 2001; Sánchez-Cordero, 2001, among others) has been reported. A decrease in diversity along an increasing elevation gradient has also been observed (Patterson et al., 1989), as it was determined for other taxa such as birds and bats (Patterson et al., 1998). Although less frequently documented, high species richness values were verified at high

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altitudes (Marquet, 1994; Novillo and Ojeda, 2014; Pearson and Ralph, 1978; Pearson, 1982). The exact shape of the relationship between species richness or diversity and elevation differs for taxa and zoogeographical area (Rahbek, 2005).

Several non-exclusive hypotheses have been proposed to explain the patterns of distribution of small mammals along elevational gradients. Among them are the reduction in the effective area, changes in biotic and abiotic parameters with elevation, isolation of montane communities and feedback between zonal communities (reviews in Brown, 2001; Lomolino, 2001; Sánchez-Cordero, 2001). Rahbek (2005) demonstrated that the spatial scale employed in the analysis can influence the perception of the patterns detected along the gradient (see also Kelt et al., 2000). The shape of the species richness, diversity, and species composition pattern along an elevation gradient – hump-shaped, monotonic decreasing or increasing – will depend on the interaction of those environmental variables. In a hump-shaped relation, the location of the peaks corresponds closely to transition zones between the main zonal habitats, and is therefore consistent with predicted patterns resulting from climate gradients and overlapping of geographical ranges within ecotones (Lomolino, 2001). The interacting influences of climate, topography and soil are primary determinants of plant distribution, so, variables such as vegetation structure and productivity also exhibit complex patterns on mountainsides (Brown, 2001).

Few studies explored the composition of micromammal fauna along environmental gradients in South America. Some of them employed a global and continental scale (Kelt et al., 2000, 1996; Ojeda et al., 2000). The others, on a small-scale analysis, were conducted in the temperate forest in the southern Chilean Andes (Kelt et al., 1994; Kelt, 1996; Patterson et al., 1989, 1990) and the forest–steppe ecotone in northwestern Patagonia (Pearson and Pearson, 1982). The small mammal fauna was also evaluated along regional latitudinal gradients (Meserve and Glanz, 1978; Meserve et al., 1991). Some scarce studies have been done about altitudinal gradients for the arid lands. Specifically for South America, the few studies were conducted along the dry Andes (Marquet, 1994; Novillo and Ojeda, 2012, 2014; Pearson, 1982).

Patagonia exhibits one of the sharpest environmental gradients known on Earth. This is due to the synergy between two factors: precipitation and temperature (Paruelo et al., 1998). This climate gradient sets the boundaries of the main vegetation types from west to east: forest, bunchgrass steppe, brush-grass steppe and bush steppe (León et al., 1998) and landscape structure (del Valle et al., 1995).

East of the Andes, gradients of many environmental variables are at least as pronounced as those on the west and are associated with a marked elevational component. Somuncurá is one of the most important and extensive plateaus from the Extra-Andean Patagonia. It even reaches heights similar to the ones detected in the mountains of the Southern Andes. Somuncurá is a Protected Natural Area that harbours a number of endemic species and is an area of high biogeographical importance for the evolution of diverse taxa (Ceï, 1969).

A consistent geographical pattern was observed for micromammal species in the main landscape divisions in Patagonia (Monjeau et al., 1997, 1998) and even according to changes in the vegetation (Pardiñas et al., 2003). In those studies at a selected large spatial scale (northern Patagonia), the Somuncurá plateau was incorporated into the analysis by only a few peripheral localities. At a smaller spatial scale, studies by Andrade (2007, 2009) in Somuncurá suggested a species turnover pattern related with elevation and high species richness as a consequence of the environmental heterogeneity and the strong elevational gradient.

The theoretical context presented by the studies cited above, is the roots that generate scientific targets we have proposed for this work.

2. Materials and methods

2.1. Study area

This project was carried out in the Protected Natural Area of the Somuncurá Plateau, a massive 25,000 km² volcanic plain located in the middle of the Extra-Andean arid Patagonia, Chubut and Río Negro Provinces, Argentina, between 41° and 43°S and between 66° and 68°W (Appendix A, electronic version only). The altitudinal gradient – between 500 and 1600 m a.s.l. – is formed by superimposed layers of successive basalt flows. The effusive core, a mountain belt called Sierra del Somuncurá (Cerro Corona, highest elevation, 1644 m a.s.l.) is in the centre of the plateau, therefore the altitude decreases towards the edges (Appendix A, electronic version only). The climate is arid, warmer in the eastern and northern faces at lower elevations and colder in the southern and western faces at higher elevations. Average annual temperature at Maquinchao, on the west of the Somuncurá plateau (888 m a.s.l.), is 9.3 °C. It is the Patagonian area with the lowest winter temperature registered, and exhibits a wide thermal range from –25 °C to above 35 °C. Mean Annual Precipitation is 187 mm (data given by DPA, Departamento Provincial de Aguas – Río Negro). For the east, average annual temperature and precipitation are 14 °C and 227 mm respectively (Dique 1 meteorological station, Valcheta, Río Negro, 190 m a.s.l., data given by DPA). Winds in the area are mainly from the west or south-west. Means for Maquinchao Station are 3.15 m/s. Upper levels remain snowy until late September with frosts even in late spring.

The vegetation units from northern Patagonia (León et al., 1998) are associated in Somuncurá with the altitudinal gradient (Beeskow et al., 1982). While the Monte Phytogeographical Province (Southern Monte, warm desert) dominates the lower levels, the Patagonian Steppe (cold desert) prevails above. These biomes gradually interchange species in a broad ecotonal area (Ecotono Rionegrino following León et al., 1998) (Appendix A, electronic version only). At lower elevations (≤450 m a.s.l.), the dominant physiognomy is typical of the Monte, with a predominance of three species of *Larrea* (*Larrea divaricata*, *Larrea nítida*, and *Larrea cuneifolia*). In the lower parts of the shrub steppe the vegetation is open and the species richness is poor, dominated by halophytes such as *Atriplex lampa* among others. As elevation increases, herbaceous elements are mixed with shrubs, forming the so-called Ecotono Rionegrino (sensu León et al., 1998). In these intermediate altitudes, shrubs typical of the Monte (i.e.: *Prosopidastrum globosum*, *Prosopis alpataco*, *Bougainvillea spinosa*, *Schinus polygamous*, and *Ephedra ochreatea*) are interspersed with those of the Patagonian steppe (*Mulinum spinosum*, *Grindelia chilensis*, and *Chuquiraga erinacea*). Among the bunchgrasses, *Stipa humilis* and *Stipa speciosa* are the dominant species. Between 800 and 1000 m a.s.l. low shrubs from the Monte can still be found, covering approximately 60% of the soil. The most abundant species of shrubs are *M. spinosum*, *Senecio mustersii*, *G. chilensis*, and *E. ochreatea*. This community disappears between 900 and 1000 m a.s.l. to give way to the full dominance of the Patagonian steppe. On the basaltic rocks, a community of *Senecio flaginoides*, *Pantacantha ameghinoi*, *M. spinosum*, and *Schinus johnstonii* develops among others. From 1200 m a.s.l., the habitat is an extensive plain covered by bunchgrasses, a feature characteristic of the Western Patagonia. The herbaceous layer is dominated by *Poa ligularis*, *S. speciosa*, *Festuca pallescens*, *Bromus setifolius*, and *Carex* sp. The shrubby steppe practically

disappears, leaving small shrubs like *Verbena* aff. *comberi*, *Senecio hatcherianus*, and *Acaena confertissima* (Beeskow et al., 1982).

2.2. Small mammal sampling

The animals considered in this study were small non-flying land mammals: rodents of families including Caviidae, Ctenomiidae, Cricetidae subfamily Sigmodontinae, and marsupials of family Didelphidae. At least two species of genus *Eligmodontia* were detected in Somuncurá, *Eligmodontia typus* and *Eligmodontia morgani* (Hillyard et al., 1997). Their identification was based on karyotype and mtDNA. Cranial measurements were the only diagnostic morphological characters taken into account to assign specimens to a correct species. Given the nature of the samples considered in this study, these taxa were regarded as *Eligmodontia* sp.

Mammals were sampled along altitudinal and vegetation gradients. A total of 22 sampling sites were performed along the only roads in the Somuncurá plateau (Appendices A and B, electronic version only). The altitudinal gradient was divided into ranges: lower than 500 m a.s.l., between 500 and 750 m a.s.l., between 750 and 1000 m a.s.l., between 1000 and 1250 m a.s.l., and higher than 1250 m a.s.l. (Appendix A, electronic version only). The vegetation gradient was divided into the main phytogeographical units following León et al. (1998) for Extra-Andean Patagonia: Southern Monte (Monte Phytogeographical Province), Monte–Patagonian Steppe ecotone (Ecotono Rionegrino) and Patagonian Steppe (Patagonian Phytogeographical Province) (Appendix A, electronic version only).

Two complementary methodologies were implemented to assess small mammal biodiversity: analysis of pellets deposited by the nocturnal raptor *Tyto alba* – a specialized predator of small mammals – and trap sampling. Both data sources were employed because of their advantages. Owls are effective predators and generate small mammals' deposits with large sample size. Pellets were successfully employed in biodiversity assessments. Even in altitudinal gradients, barn owl pellets were good indicators of the composition of rodent populations along the gradient (Travaini et al., 1997). In this sense, pellets were used to determine altitudinal patterns in the composition of small mammal assemblages and traps to explore abundance patterns along the gradient.

Pellets were decomposed and prey were identified and quantified on the basis of skulls and mandible pairs using reference collections and identification keys (Andrade, 2009). The Minimum Number of Individuals (MNI), the relative frequency, and the standardized frequency (octave) data transformation were calculated for each prey species in the owl pellet samples.

Trap sampling was conducted in April 2004, 2006, 2007 and March 2008 (Appendix C, electronic version only). This season was selected for the surveys as previous samplings confirmed that the abundance of small mammals is higher towards late summer and early autumn. Besides, higher levels in the Somuncurá plateau remain isolated because of snow storms during winter so it was impossible to make the field work during this season at all the sample localities. Sampling sites were located at every altitudinal range (500–750 m a.s.l., 750–1000 m a.s.l. and 1000–1250 m a.s.l.); one central sampling site was located around the Corona volcano (1400 m a.s.l.) (Appendices A and B, electronic version only). Sherman traps were baited with rolled oats and vanilla, visited daily and re-baited if necessary. Animals captured were identified to species, weighed, and measured. Only voucher specimens were dissected to help species identification and future studies. Standard preparation included museum skins and skeletons, liver tissues samples conserved in 96% ethylic alcohol, and stomachs preserved in 10% formalin.

Surveys were conducted with the permission of Dirección de Fauna Silvestre, Ministerio de Producción (Exp. N° 85172 – DF 2004) and Consejo de Ecología y Medio Ambiente (Res. N° 378/07), Río Negro province.

2.3. Faunal data set and spatial analysis

Multivariate analyses were used to classify sampling sites into geographical patterns. Two attributes of the pellet samples were analyzed: presence/absence and standardized frequency of small mammal species. Faunal databases were made and the Euclidean Distance Matrix employed in a cluster analysis built with the Unpaired Group Mean Average Algorithm (UPGMA). It was assumed a Cophenetic Correlation Coefficient (CCC) higher than 0.8 as a measure of cluster reliability. A correspondence analysis (CA) was used to ordinate Somuncurá localities based on the species composition and environmental variables (vegetation and altitude). To test if the altitudinal gradient would explain differences in species composition between localities (based on their ordination on the CA) a correlation analysis was made between site loadings for the first axis and the altitude. Three pellet samples collected outside the study area but near Somuncurá were incorporated into the analysis as outgroups: Laguna Blanca and Punta Este (Southern Monte, De Santis and Pagnoni, 1989) and Estancia Calcatreo (Patagonian steppes, Andrade et al., 2002; see Appendix B). To evaluate biogeographical affinities between Somuncurá small mammals and major landscape units in Patagonia, the study samples were incorporated into multivariate analysis with outgroups samples generated also by the raptor *T. alba* collected at the southern end of the Patagonian Steppes, from Santa Cruz Province (Estancia Buenos Aires, Estancia Cordón Alto and Estancia La Ascensión: Cueto et al., 2008) and Chubut province (Estancia El Rincón, this study) and at the Southern Monte (Punta Delgada: Trejo and Lambertucci, 2007; Puerto Lobos II and III: Udrizar Sauthier and Pardiñas, 2006). Multivariate and correlation analyses were performed with Past and MVSP software.

Species richness (defined as number of species) was computed for owl pellet samples localities. Trap success (defined as number of captures/number of traps per night) was employed as an estimate of the small mammal abundance at each sampling locality. The relationship (lineal or hump-shaped pattern) between these parameters and the elevation was evaluated with the SPSS software.

3. Results

3.1. Somuncurá exhibits the uppermost species richness of small mammals in Patagonia

At least 20 small mammal species were found in this study: two rodents of family Caviidae, one of family Ctenomiidae, fifteen of family Cricetidae, subfamily Sigmodontinae, and two marsupials of family Didelphidae. As far as we are concerned following the published literature, this is the uppermost species richness compared to other sites of similar area in Patagonia (Andrade, 2009), holding 71% of the 21 species of Cricetidae, 100% of the small Didelphidae (*Didelphis albiventris* was not registered in this study because it cannot be considered a small mammal), 100% of the Caviidae (*Dolichotis patagonum* inhabits Somuncurá but was not included in this study because it is not a small mammal), cited for the whole Patagonia (Barquez et al., 2006).

3.2. Species composition changes with elevation

Cluster analysis on the small mammal presence/absence matrix (CCC = 0.9547) resulted in three discrete groups of sites based on

the similarity in species composition, discriminating areas located below 750 m a.s.l. (Group I), between 750 and 1000 m a.s.l. (Group III) and above 1000 m a.s.l. (Group II, Fig. 1A). These groups are associated with the main Phytogeographical units in Somuncurá. Group I consists of pellet assemblages collected in the Southern Monte, while Group II represents those from the Patagonian Steppe, and Group III associated areas located in the Monte–Patagonian Steppe ecotone.

The correspondence analysis (CA) applied to the same matrix shows consistency with the cluster analysis. Axis 1 and 2 explain 70.14% of the total variance. Axis 1 explains variation in altitude: localities are arranged along this axis following the altitudinal gradient. The same three groups were obtained in the ordination in the CA space (Fig. 2A). The assemblages from the Southern Monte and lower levels are characterized by the species *Akodon iniscatus*, *A. molinae*, *Calomys musculus*, *Oligoryzomys longicaudatus*, *Galea musteloides*, *Graomys griseoflavus* and *Thylamys pallidior* (positive scores in the axis 1 of the CA). The assemblages from the Patagonian Steppe and higher levels are characterized by the disappearance of species from the Monte and composed by *Abrothrix longipilis*, *Abrothrix olivaceus*, *Chelomys macronyx*, *Euneomys chinchilloides*, *Lestodelphys halli* and *Notiomys edwardsii* (negative scores in axis 1 of the CA). The assemblages from the Monte–Patagonian Steppe ecotone area at intermediate altitude were grouped in the middle of the CA, between group I and II, and are characterized by the absence of own species but sharing species with localities at higher and lower levels in the plateau. Among the first are *A. longipilis*,

A. olivaceus, *L. halli* and *N. edwardsii*; among the second *A. iniscatus*, *G. musteloides*, *G. griseoflavus* and *T. pallidior*.

Reithrodon auritus and *Microcavia australis* were arranged in a central location in the CA space (0 scores in the axis 1 and 2). These are widely distributed species along the gradient, so they are not relevant to discriminate the groups. In the case of *Loxodontomys micropus*, its central ordination is related with the representation in only one study site. For the case of *Eligmodontia* spp. and *Ctenomys* spp., their central arrangement in the CA space must be due to the taxonomical uncertainty.

The significance in the correlation analysis between the real altitude of the sampling sites along the gradient and the scores obtained for the first axis in the CA ($r = -0.8952$; $p < 0.0001$) confirms that the altitudinal gradient explains the differences in species composition.

The CA and cluster analysis applied to the standardized frequency matrix shows the existence of the same three groups (Figs. 1B and 2B). Two subgroups were observed in the cluster in Group I. They reflect the real arrangement of the areas along the altitudinal gradient. Subgroup *a* segregates assemblages collected at elevations below 500 m a.s.l. and subgroup *b* those samples between 500 and 750 m a.s.l. along the gradient. Frequencies of *G. musteloides*, *C. musculus*, *O. longicaudatus* and *A. iniscatus* increase towards higher levels as compared with lower levels (subgroup *b*, positive scores in the axis 2 of the CA). These subgroups are also ordered along an east–west vegetation gradient in the southern Monte.

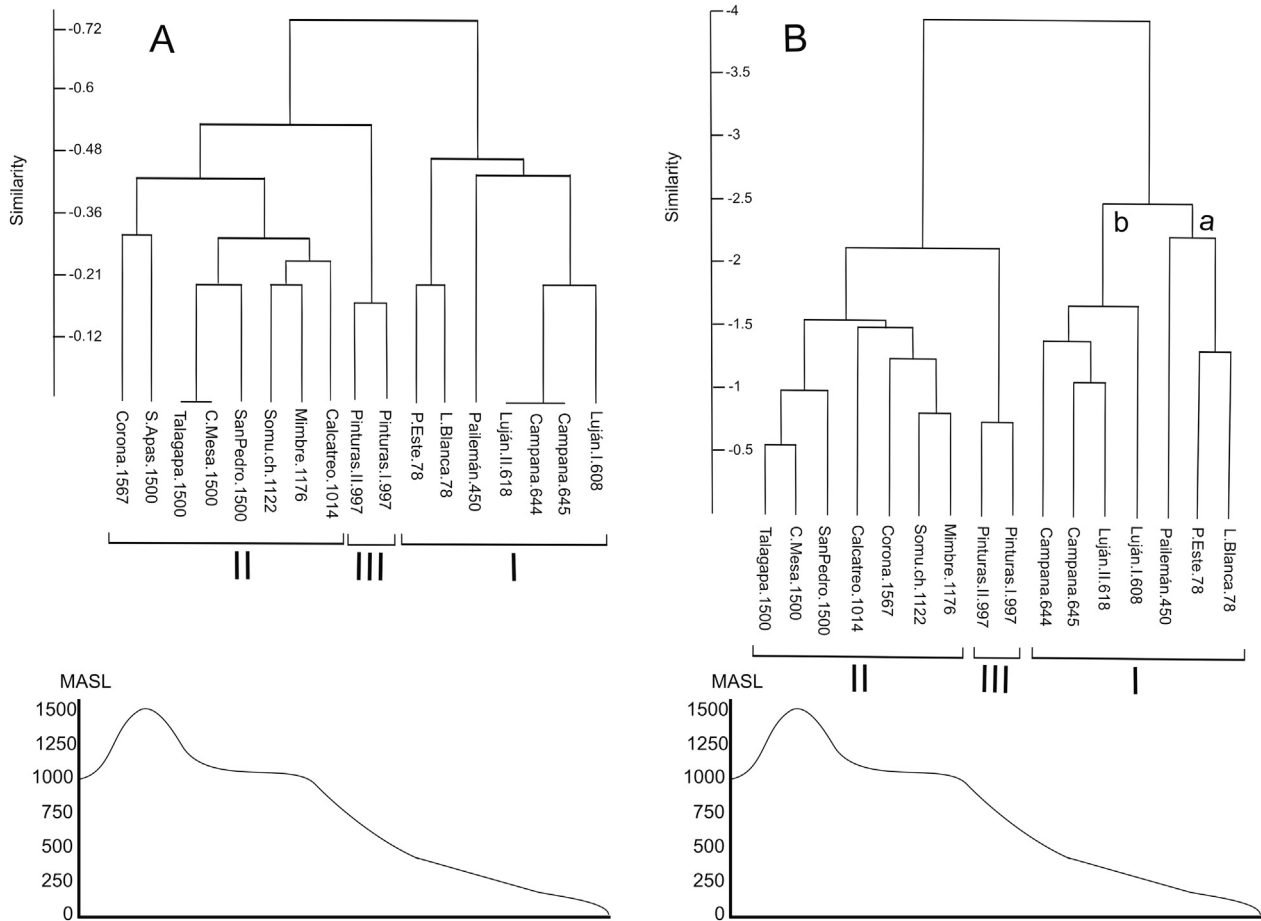


Fig. 1. Results of cluster analyses based on small mammal species composition in pellet sampling localities and their correspondence with the altitudinal gradient. (A) Presence/absence matrix and (B) standardized frequency matrix. Groups I, II and III are pellet assemblages collected in the Southern Monte, the Patagonian Steppes and the Monte–Patagonian Steppe Ecotone respectively. Subgroups in Group I segregate assemblages collected below 500 m a.s.l. (a) and between 500 and 750 m a.s.l. (b) along the gradient.

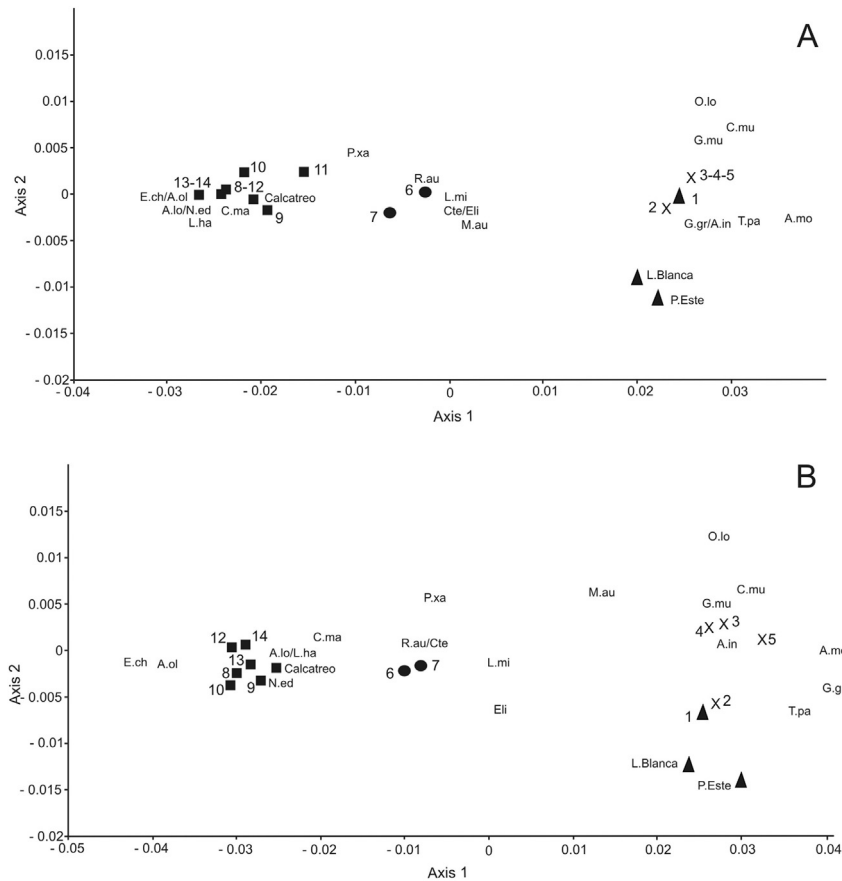


Fig. 2. Ordination of pellet sampling localities produced by a correspondence analysis based on small mammal species composition. (A) Presence/absence matrix and (B) standardized frequency matrix. The assemblages from the Southern Monte and lower levels are pointed out with crosses (localities between 750 and 500 m a.s.l.) and triangles (localities lower than 500 m a.s.l.), those from the Patagonian Steppes and higher levels (above 1000 m a.s.l.) are pointed out with squares and those from the Monte–Patagonian Steppe Ecotone at intermediate altitude with circles. Numbers correspond to the locality numbers in [Appendices A and B](#). A.lo = *Abrothrix longipilis*; A.ol = *A. olivaceus*; A.in = *Akodon iniscatus*; A.mo = *A. molinae*; Eli = *Eligmodontia* sp.; O.lo = *Oligorizomys longicaudatus*; C.mu = *Calomys musculus*; N.ed = *Notiomys edwardsii*; E.ch = *Euneomys chinchilloides*; P.xa = *Phyllotis xanthopygus*; R.au = *Reithrodon auritus*; L.mi = *Loxodontomys micropus*; C.ma = *Chelemys macronyx*; G.gr = *Graomys griseoflavus*; Cte = *Ctenomys* sp.; M.au = *Microcavia australis*; G.mu = *Galea musteloides*; L.ha = *Lestodelphus halli*; T.pa = *Thylamys pallidior*.

3.3. Small mammal abundance is correlated with elevation

A clear pattern was observed by a polynomial correlation between the abundance of small mammals and elevation. An increase in the small mammals abundance was registered at intermediate levels (between 750 and 1000 m a.s.l.) while it decreases towards higher and lower levels ($R^2 = 0.807$, $N = 7$; [Fig. 3A](#)).

3.4. Species richness is correlated with elevation

We found no significant lineal correlation between species richness for owl pellet samples and elevation ($R^2 = 0.04$). However a clear hump-shaped pattern was supported by a polynomial correlation ($R^2 = 0.6243$, $N = 14$; [Fig. 3B](#)).

3.5. The altitudinal pattern of species assemblage mirrors the latitudinal patterns

Multivariate analysis showed three assemblages associated with the altitudinal and latitudinal pattern: species typical of the southern Patagonian steppes and higher elevations, species typical of the northern Monte vegetation and lower areas, and an ecotone in intermediate altitudinal levels with a mixed assemblage ([Fig. 4](#)). The typical Monte steppe is characterized by *A. iniscatus*, *A. molinae*, *E. typus*, *G. griseoflavus*, and *T. pallidior*, while the species in the typical Patagonian steppe are *A. olivaceus*, *A. longipilis*, *E. morgani*, *E.*

chinchilloides, *L. halli*, *Phyllotis xanthopygus*, and *Reithrodon auritus*. The location of the outgroups from the Monte and Patagonian steppes in the ordination space ([Fig. 4](#)) depicts the biogeographical affinities with the major landscape units in Patagonia.

4. Discussion

This is the first study that explored the altitudinal gradient in Argentine Patagonia. We focussed particularly in the central basaltic plateaus of the desert Extra-Andean region, particularly in the Somuncurá plateau, by researching the effects produced by the altitudinal gradients on the small mammal assemblages' composition.

4.1. Species richness

It is important to point out that the only continuously distributed taxa along the whole gradient (*Eligmodontia* sp., *Ctenomys* sp., *Microcavia australis* and *Reithrodon auritus*) are likely to conceal more than one. In the case of *Eligmodontia* sp. we can state that two species live in the plateau ([Hillyard et al., 1997](#); [Sikes et al., 1997](#)): *E. morgani* is likely to be in association with the Patagonian steppe while *E. typus* with the Monte ([Monjeau et al., 1997](#)). In the other cases, the confusing and changing taxonomy and the lack of recent systematic studies suggest that we are dealing with more than one species. At least five species of the genus *Ctenomys* were cited for

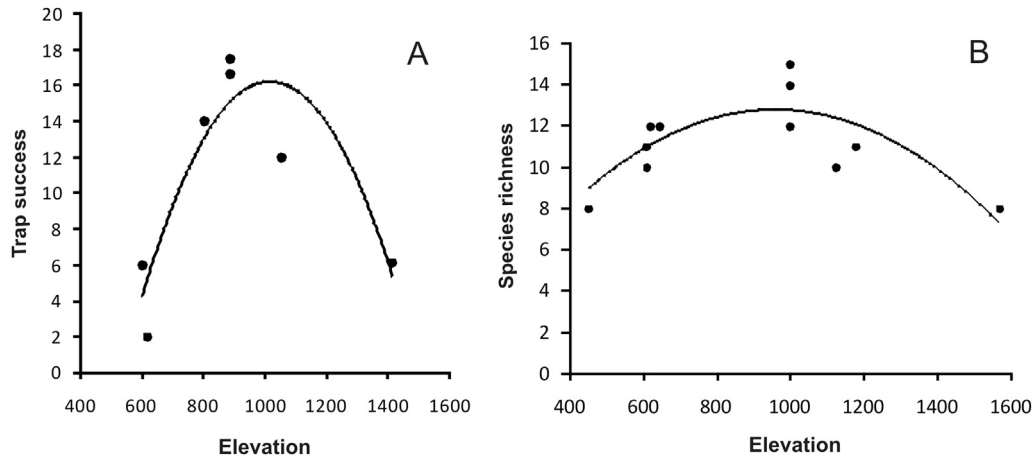


Fig. 3. Abundance, estimated by trap success (A) and species richness (B) of small mammals along the altitudinal gradient.

northern Patagonia provinces (Barquez et al., 2006), taxonomy that mainly is based on karyotypical data. Therefore, the species richness of Somuncurá is likely to be higher than 20, and the gradient which in itself is already sharp is very likely to be reinforced by new findings.

4.2. Spatial variation of small mammal assemblages

Differences in species composition along the gradient were evident. The abrupt altitudinal gradient in the Somuncurá plateau shape up the small mammal's assemblage composition along the gradient. At the same time, this influences the plant communities in such a way that small mammals and vegetation respond jointly to height variation, as proposed by Monjeau et al. (1998) in relation to the hierarchy of landscape structure.

The main change in the small mammal fauna in the plateau was recorded around the 1000 m a.s.l. The species which are clearly typical of the warmer Monte desert disappear and give place to a typical colder Patagonian desert fauna. The altitudinal ranges of most of the species overlap in a vast ecotone area at the intermediate levels (between 750 and 1000 m a.s.l.) in which the vegetation is typical of the Monte–Patagonian steppe ecotone as defined by León et al. (1998). Similar results were obtained for plant communities. Beeskow et al. (1982) concluded that there is a

successional transition between the Monte and the Patagonian steppe vegetation that depends on the elevation.

It is important to point out the relevance of the analysis scale used in patterns detection. As it decreases, the ecotone status shown in the Somuncurá plateau regarding the main landscape units in Northern Patagonia (Monjeau et al., 1997, 1998) became a more complex and highly heterogeneous system, with flora and fauna variations along its altitudinal gradient.

4.3. Species richness and abundance related to elevation

Relative abundance and richness of small mammal assemblages show a definite pattern along the Somuncurá plateau altitudinal gradient. The two parameters clearly increase at the intermediate levels and decrease towards the system upper and lower heights. This hump-shaped pattern is similar to the pattern shown by non-flying small mammals in mountain ranges all over the world (Li et al., 2003; Md Nor, 2001; Sánchez-Cordero, 2001, among others). Although latitudinal gradients have been widely documented, we found a lack of references comparing altitudinal gradients globally, much less in deserts. This lack of references in the literature reviewed invites us to assume that our study is one of the few who have addressed the issue of altitudinal gradients in mammals concerning desert environments. For the dry Andes of

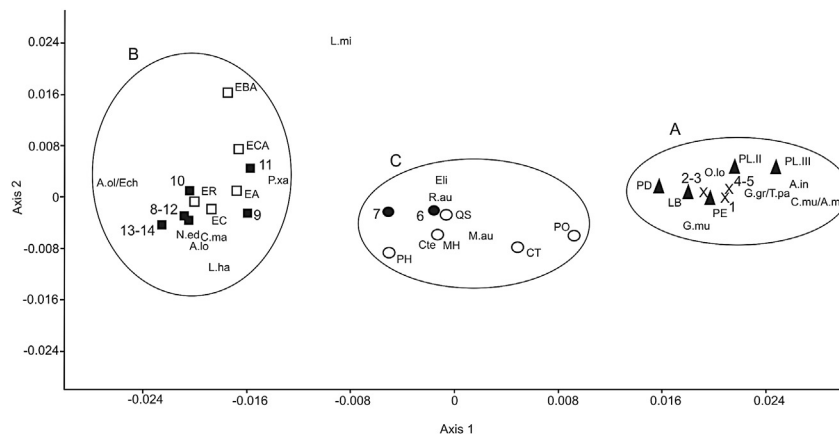


Fig. 4. Correspondence analysis based on Somuncurá localities, Monte and Patagonian steppes outgroups and fossil localities from Buenos Aires province. Groups A, B and C are those from Fig. 5. Crosses: Monte Somuncurá localities; Triangles: Monte outgroup localities; Filled circles: Monte–Patagonian Steppe Ecotone localities; Empty circles: fossil localities; Filled squares: Patagonian steppes Somuncurá localities; empty squares: Patagonian steppes localities from Río Negro, Chubut and Santa Cruz provinces. Numbers correspond to the locality numbers in Appendices A and B. PLII, PLIII: Puerto Lobos II and III; PE: Punta Este; LB: Laguna Blanca; PD: Punta Delgada; EBA: Estancia Buenos Aires; ECA: Estancia Cordón Alto; EA: Estancia La Ascensión; ER: Estancia El Rincón; EC: Estancia Calcatreo; PH: Punta Hermengo; PO: Paso Otero; CT: Cueva Tixi; QS: Quequén Salado; MH: Monte Hermoso.

Perú, Argentina and Chile, a positive and monotonic relationship between species richness and altitude (Marquet, 1994; Novillo and Ojeda, 2014; Pearson, 1982) and a peak at middle elevations for the small mammal's abundance (Novillo and Ojeda, 2012) was proposed. That is, species richness increases with altitude between the Pacific coastal desert (hot desert) and the Puna (cold desert, Marquet, 1994). Also, richness of endemic species is positively associated with elevation (Novillo and Ojeda, 2012). High diversity values and endemic species for small mammals were associated with historical speciation events at a high altitude centre of biotic diversification in the Andes (Marquet, 1994; Novillo and Ojeda, 2012). The increase in rainfall with elevation is paralleled with changes in plant cover and physiognomy. Therefore, unlike what happens in Somuncurá, the historical pattern observed in the richness and diversity of small mammals in dry Andes is maintained by features related with gradients of biotic and abiotic parameters.

Lomolino (2001) puts forward four main possible explanations for altitudinal gradients of richness and diversity which correlate with the features of mountain systems: a) area gradient, b) geographical isolation of communities, c) abiotic parameters gradient and d) feedback among communities at different levels of the gradient. We will discuss these possible explanations for the case of the Somuncurá plateau. Regarding the area gradient hypothesis (a), which predicts that species richness will be directly proportional to the total area of each altitudinal level, in Somuncurá the total area is larger at lower levels and decreases towards the upper levels, whereas species richness is higher at intermediate levels (Fig. 3B). For this reason, this hypothesis is not considered as an adequate explanation of the pattern observed. The second hypothesis (b) predicts an island effect as the cause of the low specific richness observed at higher levels in the mountain systems. Small mammal species are not isolated in Somuncurá. Small mammal communities at upper levels relate with the fauna of Patagonia west and south while the assemblages at the lower levels relate with the ones from the east and north (Fig. 4). This hypothesis is therefore also excluded as a plausible explanation.

The hypotheses (c) and (d) require more discussion. If we think in a "climatic" gradient we need to consider at least precipitation and temperature. There is no rainfall gradient in Somuncurá, it is low and constant all over the area. However, temperature decreases with height. Because species richness is favoured when the mean values of the environmental variables lie within the optimal range for the physiological needs of the species, low temperatures act as strong selective filters having a direct effect on the number of species able to survive in harsh conditions. Extremely cold temperatures at high latitudes or elevation are the «hidden guillotine» that may indeed reduce the proliferation of species as proposed by Monjeau et al. (2009). Maybe Somuncurá is not high enough (not harsh enough) to show these influence of temperature on species richness. However, this hypothesis may explain why at the intermediate levels, approximately between 800 and 1000 m a.s.l., there is a peak in species richness and a replacement of the warm Monte desert fauna and flora by that of the cold Patagonian desert.

The hypothesis (d) predicts that the increase on richness and diversity is produced at the intermediate levels as a consequence of the overlap in the distribution of lower and upper species in the altitudinal gradient. Combined with the temperature effect (hypothesis c), this is the most appropriate explanation to the results obtained in Somuncurá. The differential tolerance to elevation among the different small mammal species and the consequent overlapping in the distribution areas of most of the species between 750 and 1000 m a.s.l. (Andrade, 2009), leads, therefore, to an increase in richness. Brown (2001) proposed the last two hypotheses amplify each other and may be the main reason for species richness

on high mountains in desert regions, where species that can tolerate the hot arid lowlands cannot exist in the cold higher environments but many species overlap at intermediate elevations where conditions are not so extreme. The pattern in which the peak in species richness is a consequence of the overlapping ranges of species with different distributional ranges was termed for the case of latitudinal gradients as mid-domain effect (see McCain, 2003 for a discussion about this topic in relation with latitudinal gradients in North American desert rodents). The increase in species richness in the Somuncurá plateau is then the result of the overlapping of two similarly rich and diverse areas. In this ecotonal area, vegetation heterogeneity increases and moisture and water availability is higher than in upper and lower levels, leading also to a rise in small mammals total abundance at these intermediate levels.

The results of this study concur with the studies that state that altitudinal and rainfall gradients are within the most important factors to the structuring of small mammal communities in Patagonia (Meserve et al., 1991; Patterson et al., 1990; Pearson and Pearson, 1982, among others). Monjeau et al. (1997, 1998) point out that in the arid Extra-Andean steppes, where rainfall is low and homogeneous in comparison with the western wide variability along the transition between the forest and the steppe, altitude is the main predictor of small mammal assemblages' composition.

4.4. Biogeographical affinities

Small mammal assemblages from the Somuncurá plateau show clear affinities with major landscape units in Patagonia: those from the lower levels with the ones from the eastern Southern Monte and assemblages from the upper levels share species with the western and southern Patagonian steppes, in Santa Cruz province (Figs. 4 and 5). The northwest–southeast biogeographical gradient detected in the composition of small mammal assemblages (Monjeau et al., 1998, 1997; Pardiñas et al., 2003) appears in the Somuncurá plateau in a more restricted geographical area and related to the steep slope in the plateau. As it has already been highlighted, in the Somuncurá plateau and all over the Extra-Andean Patagonia, rainfall is low and uniform. However, there is a sharp temperature gradient which reflects itself in a steady decrease in the annual average temperature along the height gradient. These results, as a whole, allow us to very clearly state that in the arid Extra-Andean Patagonia temperature is the main factor to the structuring of small mammal communities. This is the reason why height and latitude have a similar effect in the species composition of small mammal assemblages. On the one hand, the air gets colder as we ascend towards higher altitudes because it expands in response to reduced pressure, undergoing what is called adiabatic cooling (McArthur, 1984). The adiabatic cooling rate of dry air with increasing elevation is approximately 10 °C/1000 m (Flohn, 1969). On the other hand, the air gets colder when latitude increases because the same quantity of solar radiation must cross a thicker layer of the filtering atmosphere and spread over a greater surface area (Brown and Gibson, 1983). The cooling rate, considering winter temperatures, is about 1 °C per degree of latitude towards the poles. If we consider that a 100 m ascent along the altitudinal gradient is equivalent to moving 111 km to the south, in order to come across similar small mammal assemblages of the Patagonian steppe you should move approximately 1000 m upwards in the inner basalt plateaus or travel approximately 1000–1100 km to the south.

The same spatial pattern can be tracked throughout past climatic changes: cold and dry environmental conditions similar to those of Patagonia today extended 750 km farther north-eastwards during the Late Pleistocene and Early Holocene, until 8500 yr B.P. (Iriondo and Garcia, 1993), leading to desert vegetation covering

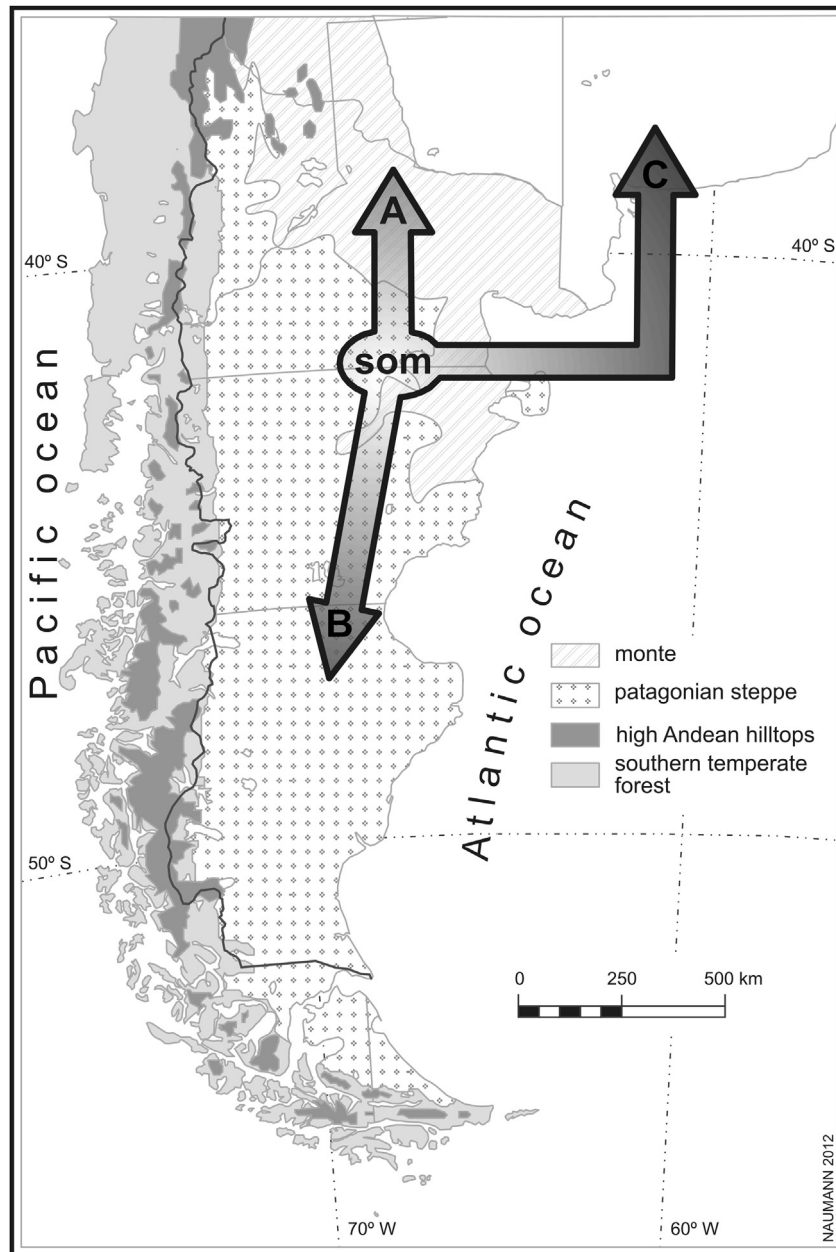


Fig. 5. Biogeographical affinities of small mammals. Som = Somuncura. A = Affinities between lowland assemblages with communities inhabiting Monte ecoregion, to the north. B = Affinities between assemblages from uplands with communities typical of the Patagonian steppe ecoregion, to the south. C = Affinities between the current species composition of Somuncura ecotone with the fossil record.

the present Argentine Pampas (Tonni et al., 1999). These authors proposed, based on a combination of different sources of evidence, a temperature drop of perhaps 5 °C was the origin of that environmental scenario. The Patagonian marsupial *L. halli* and the rodents *E. typus* and *Microcavia australis*, typical of arid and semiarid regions, extended to the eastern and northern Pampas (Alberdi et al., 1989; Pardiñas, 2001; Tonni and Fidalgo, 1982; Tonni et al., 1988, 1999). *Reithrodon auritus*, a frequent species in the Extra-Andean Patagonian steppe was dominant in some Buenos Aires Late Pleistocene localities (Punta Hermengo: Tonni and Fidalgo, 1982). Small mammal assemblages from fossil localities dated between Late Pleistocene and Early Holocene from Buenos Aires province (Punta Hermengo: Tonni and Fidalgo, 1982; Paso Otero: Prado et al., 1987; Cueva Tixi: Tonni et al., 1988; Quequén Salado: Alberdi et al., 1989; Monte Hermoso: Pardiñas, 2001) show

affinities with the Somuncurá Monte–Patagonian Steppe ecotone, at intermediate elevations (Figs. 4 and 5). The late Pleistocene phenotype of the *L. halli* remains (Cueva Tixi, Buenos Aires hilly area: Prado et al., 1985) shows a clinal size decrease as a physiological response to temperature.

These results, taken as a whole, allow us to conclude that variation in the composition of small mammal assemblages in Patagonia, be that in space or time, latitude or altitude, is driven by temperature.

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Appendix A. Supplementary material

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.jaridenv.2014.02.004>.

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