Unraveling the patterns of small mammal species richness in the southernmost aridlands of South America

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ABSTRACT

Understanding the patterns of species richness is a critical aspect for the conservation of biodiversity. Patagonia is located southern of 40°S, mostly covered by an aridland and is the only area of the Southern Hemisphere (excluding Antarctica) that allows the study of a high-latitude terrestrial biota. In this work we describe the spatial variation of species richness of the non-flying small mammal assemblages, covering ~12° of latitude in Patagonia. We analyzed 100,000 specimens and the relation between environmental variables and small mammal richness. Species richness decreased southwards and eastwards and turnover of species was not observed. We found high richness values in the north of Patagonia and high correlations between species richness and environmental variables in the south. We suggest that current species richness distribution in Patagonia is the result of historical (glacial history and main rivers acting as geographic barriers) and current climatic factors (e.g., temperature) along with species ecology. Our results highlight the importance of northern Patagonia as a reservoir of diversity across time and as most of the glacial refuges were potentially located on this area, we might expect it to be more severely impacted by current global warming.

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

Charles Darwin (1839:215)

1. Introduction

Biodiversity loss has increased during last decades, mostly driven by the modification of natural ecosystems by human activities (e.g., Rohde, 1992; Ricklefs and Schluter, 1993; Kerr, 1997; Gaston, 2000; Ceballos and Ehrlich, 2002; Barnosky et al., 2011; Woinarski et al., 2015). Understanding the spatial distribution of species richness is a critical point for the conservation of global biodiversity (e.g., Gaston, 2000; Orme et al., 2005). Spatial diversity

patterns are among the most addressed and intriguing issues in ecology and biogeography (Brown, 2014). In southern South America the spatial distribution of biodiversity was documented for some groups of organisms (e.g., birds in Bini et al., 2004; mammals in Tognelli and Kelt, 2004; mammals and butterflies in Samaniego and Marquet, 2009). However, there is no consensus about the factors and mechanisms that control and regulate it (Shmida and Wilson, 1985; Rohde, 1992; Kerr and Packer, 1997; Hortal et al., 2008). In fact, biodiversity patterns are modeled by several causes, hence trying to explain the variation on species richness by only one factor is usually not enough. The final cause of these patterns appears to be due to the interaction of the physiology and ecology of the involved species, to the environmental variability -both past as current (e.g., Pianka, 1966; Owen, 1990; Kerr and Packer, 1997; Gaston, 2000; Marquet et al., 2004) - and to the scale of the analysis (Ojeda et al., 2000; Sarr et al., 2005; Samaniego and Marquet, 2009).

Patagonia is one of the few territories beyond 40°S holding complex biological communities. This feature makes this region the only area of the Southern Hemisphere (excluding Antarctica) that allows the study of a high-latitude terrestrial biota (León et al., 1998; Oesterheld et al., 1998; Pardiñas et al., 2003; Soriano et al.,

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1983; Lessa et al., 2010). This region shows a complex mosaic of vegetation units, including tundra in its southernmost end, shrub steppes in central and northern areas, herbaceous steppes in the Andean piedmont and rainy cold forests in a narrow fringe to the west (Paruelo et al., 1998a). Most part of this region is a dryland (<300 mm/year precipitation), encompassing ~730,000 km^2 (León et al., 1998; Soriano et al., 1983).

There are 84 species of mammals living in Patagonia and about 48 are terrestrial small mammals (<250 g), including mostly rodents, but also four marsupials and one armadillo (e.g., Pardiñas et al., 2011; Lessa et al., 2012). Numerous studies were carried out on their ecology, systematics and geographic distribution (e.g., Osgood, 1943; Mann Fischer, 1978; Pearson and Pearson, 1993; Monjeau et al., 1998; Pardiñas et al., 2003, 2011; Lessa et al., 2010). However, the exploration of the specific richness of their assemblages has only been addressed at local scale (Pearson and Pearson, 1982; Pardiñas et al., 2003; Monjeau et al., 1998; Andrade and Monjeau, 2014).

Northern and southern portions of Patagonia had differential glacial histories, being those territories south of 46−47°S most deeply and widely affected by the Quaternary glacial cycles (see Rabassa, 2008). The biological imprint of these differences are illustrated by the phylogeographic breaks shown by several small mammals (Himes et al., 2008; Lessa et al., 2010; Pardiñas et al., 2011) and in the virtual absence of vertebrate refugia in the southernmost mainland (Sérsic et al., 2011 and the references therein). Late Pleistocene glaciation had a dominant role in performing present-day diversity and distribution of vertebrates, especially at high latitudes (Taberlet et al., 1998; Araujo et al., 2008; Fløjgaard et al., 2011; Srinivasan et al., 2014). During Plio-Pleistocene glacial advances, most of the Patagonian Andean ranges and southernmost mainland were under ice or experienced cryogenic processes associated with the episodic occurrence of permafrost (Trombotto, 2008), making these areas inhospitable for life. Following glacial retreat and the return of suitable conditions, species would be expected to disperse southward from its glacial refugia, mostly located in northwestern Patagonia and south-central Chile (Lessa et al., 2012). As a working hypothesis, we expect that the current pattern of species richness be mainly the result of the interplay between the differential degree of glacial impact over the territory and the dispersal ability of each species; thus following glacial retreat, species could have recolonized southern Patagonia to different extents based on ecological traits. If this hypothesis is true we can anticipate the following findings as latitude increases: i) a reduction in small mammal species richness; ii) a stronger influence of abiotical than biotical variables in structuring the communities, especially at southern latitudes; iii) a low species turnover, from north to south, in small mammal assemblages. In this scenario the potential barrier effect of the main rivers that dissect from west to east the Patagonian territory, specially taking in mind their major expression during postglacial times (Ruzzante et al., 2011), deserves attention.

The main objectives of this work were to describe, based for first time on a very large sampling approach, i) the spatial variation of species richness of the non-flying small mammal assemblages (marsupials and rodents), covering ~12° of latitude in continental Patagonia, and ii) the potential association between species richness, environmental variables and historical factors, in order to identify those variables that most strongly influence the current spatial distribution and richness of these mammals.

2. Material and methods

Study area and data sources: This study was carried out in continental Patagonia, which is limited in the North by Barrancas-Colorado river (~38°S), in the South by Magellan Strait (~52°S), in the West by the Andean piedmont and in the East by Atlantic Ocean. This region encompass four major phytogeographic units, roughly from northeast to southwest, the Espinal Phytogeographical Province (P.P.), the Monte P.P., the Patagónica P.P. and the Subantartic P.P. (Cabrera, 1971; León et al., 1998; Burkart et al., 1999); the first three are mostly composed by steppe vegetation whereas the latter includes temperate-cold *Nothofagus* forest. The climate in Patagonia is temperate to cool-temperate and it is mainly dominated by constant west winds (Paruelo et al., 1998a). Precipitation is increased during winter and the northeastern and the southern areas of the region are also affected by air masses coming from the Atlantic Ocean, making precipitation even more seasonal. Mean annual temperate ranges from 12 °C in the northwest to 3 °C in the south (Paruelo et al., 1998a). Localities for small mammals (<250 g, including marsupials and rodents) assemblages were derived from the analysis of fresh owl pellet samples (mostly produced by Barn Owls, *Tyto alba*). We also included previous owl pellets analyses from literature (e.g., Massoia and Pardiñas, 1988; De Santis et al., 1994; Teta et al., 2002; Pardiñas et al., 2009). The Barn Owl is a cosmopolitan species widespread in Patagonia, whose diet is mainly based on small mammals (e.g., Andrews, 1990; Taylor, 1994 and the references therein; Bellocq, 2000). Although trapping is the most common method used to address small mammal assemblages, owl pellet analysis is an indirect approach extensively used in assessing small mammal distribution across geographical gradients over large areas (e.g, Moreno and Barbosa, 1992; Clark and Bunck, 1991; Millán de la Peña et al., 2003; Torre et al., 2004; Heisler et al., 2016). The use of owl pellets as a methodological tool requires a minimum amount of pellets in order to estimate the frequency of small mammals in a reliable way (De Santis et al., 1994; Yom-Tov and Wool, 1997; Millán de la Peña et al., 2003). Owl pellet analysis would provide a better picture of reality in detecting general trends of small mammal assemblages associated to landscape changes (Millán de la Peña et al., 2003); in addition, this methodology allow us to access a huge amount of data taking a relatively short period of time. It is important to note that this amount of information is almost impossible to collect trough trapping, due to the extension of the involved territories and the economic costs that would require a field-work project like this. Studied owl pellets were disaggregated with hot water and craniodental material was recovered by hand and identified to the finest taxonomic level using literature (e.g., Hershkovitz, 1962; Pearson, 1995). Taxonomy follows Wilson and Reeder (2005) and Patton et al. (2015). For each studied sample, the minimum number of individuals (MNI) was calculated as a relative abundance measurement (see Grayson, 1984; Lyman, 2008). To represent the average foraging area of owls, all samples collected in the same point (= locality) or in a radius up to 3.2 km were added up, using gvSIG software (1.10 version; gvSIG Association, 2011). This radius was based on the average radius of the home range calculated for owls (Smith et al., 1974; Bellocq, 1993; Taylor, 1994; Bennett and Bloom, 2005).

Sample size and matrix construction: In order to avoid those biases associated to the samples size (measured as MNI), rarefaction analysis was applied using R software (2.15.1 version, Kindt and Coe, 2005; Oksanen et al., 2011; R Development Core Team, 2012). With this approach the sample size bias in the analysis can be minimized and small mammal species richness can be compared between sites (Legendre and Legendre, 1998; Gotelli and Colwell, 2001). We found that the expected owl pellet sample size was of 90 individuals (Appendix 1, electronic version only), which allowed us to compare those localities with MNI ≥ 90 and different sample size (i.e., total MNI), avoiding bias in the number of recorded species. Regression analyses between sample size and species richness

were done for all samples (N = 393) and for those samples with MNI ≥ 90 (N = 205). The relation between sample size and species richness was strong and significant when all samples were considered (R^2 = 0.74, p < 0.001), suggesting that species richness is not estimated accurately with MNI < 90; in turn, this relation was weak for samples with MNI ≥ 90 (R^2 = 0.15, p < 0.001), supporting the fact that a sample size of MNI ≥ 90 is adequate for the analysis and comparison of species richness in the study area. Thus from an original data matrix composed by 25 taxa and a total of 393 data points, a subset of 23 species and 205 localities was retained for subsequent analyses (see below). Two rare caviomorph rodents, *Octodon bridgesii* and *Tympanoctomys kirchnerorum* were excluded from the remainder analyses because these species occur exclusively in samples with MNI <90 (Appendix 2, electronic version only).

To test our hypothesis about the differential histories of northern and southern Patagonia, data was divided into three sets as follows; 1) all localities, 2) localities north of the Deseado river (ca. 47°S), and 3) localities south of the Deseado river. This river is located in the north of Santa Cruz province and this procedure was follow to analyze the data in more detail, facilitating their comparison and in order to detect any pattern of species richness associated to the glacial history of Patagonia, which was more intense south of this river (Rabassa, 2008) and due to several sigmodontine rodents show a phylogeographic break in this austral sector (Lessa et al., 2012).

Species richness patterns and variable analyses: To explore the association of environmental variables and small mammal richness, mean pixel values of each environmental layer were extracted for each locality using gvSIG software (1.10 version, gvSIG Association, 2011). The environmental variables consisted of digital layers of high resolution as follows. The variables Croplands and Pasture include percentage of land covered by crops and agricultural activities (http://sedac.ciesin.columbia.edu/es/aglands.html; Ramankutty and Foley, 1999). Vegetation Continuous Fields is a product from MODIS (Moderate Resolution Imaging Spectroradiometer) sensor (http://glcf.umiacs.umd.edu/): this layer comprises the period from November 2000 to November 2001, presents a spatial resolution of 500 m and shows the percentage of vegetation cover (bare soil, herbaceous and tree cover; Hansen et al., 2003). Climatic variables available at WorldClim Global Climate Data (http://www.worldclim.org/current) and including monthly mean temperature, monthly mean precipitation and 19 bioclimatic variables derived from the combination of temperature and precipitation. These layers have a spatial resolution of 1 km (Hijmans et al., 2005b). Data for elevation were extracted from the Global 30 Arc Second Elevation Data Set (GTOPO30), developed by the U.S. Geological Survey EROS Data Center (http://edcwww.cr.usgs.gov/landdaac/gtopo30/). This is a Digital Elevation Model (DEM) regularly spaced at 30-arc seconds (Gesch et al., 1999). Global Production Efficiency Model: Summed Annual Global NPP from Advanced Very High-Resolution Radiometer (AVHRR; http://glcf.umiacs.umd.edu/; Prince and Goward, 1995; Prince and Small, 2003). This layer comprises the period 1981 to 2000, presents a spatial resolution of 8 km and shows global net primary production. Global Land Cover Product from Advanced Very High-Resolution Radiometer (AVHRR) is available at http://glcf.umiacs.umd.edu/ (Hansen et al., 1998). Finally, Normalized Difference Vegetation Index (Baldi et al., 2008), biogeographic provinces (Cabrera and Willink, 1973), wind speed, relative humidity, precipitations, mean temperature, diurnal temperature range, wet day frequency (New et al., 2002) and distance to the nearest river (calculated on the basis of shapefiles from IGN; Instituto Geográfico Nacional, 2010) were also included. In order to avoid collinearity and redundancy we selected among the above mentioned

environmental variables using Spearman's correlation coefficient (Zuur et al., 2007). A coefficient ≥0.75 was used to identify highly correlated variables following similar procedures (Rissler et al., 2006; Martínez and Di Cola, 2011) and the variables that we considered more biologically meaningful were chosen, discarding the others. Among the environmental variables, 16 were selected (see Appendix 3 for correlation coefficients ≥ 0.75, electronic version only). To evaluate which environmental variables are most related to the geographic distribution of small mammal diversity, Spearman's correlations indices were calculated (Zuur et al., 2007) between species richness and selected environmental variables, latitude, longitude and altitude.

Finally, generalized linear models (GLM; McCullagh and Nelder, 1989; Nelder and Wedderburn, 1972; Zuur et al., 2007) were run using the centered and squared variables and including them as fixed terms in the full model. Prior to multivariate modeling, preliminary univariate analyses were run for each explanatory variable up to quadratic terms. With this purpose, those sites separated less than five kilometers were joined, and those with MNI ≤90 were joined to sites with NMI higher than 90. Species richness was recalculated for these new arrangement of the sites and used as the response variable in a GLM as a function of environmental variables (McCullagh and Nelder, 1989). Poisson error distribution and log function as a link between the response variable and the linear predictor were used in the modeling. The explanatory variables used for these models were described above and included: Climatic variables from WorldClim Global Climate Data (Hijmans et al., 2005b): BIO1 (Annual Mean Temperature), BIO8 (Mean Temperature of Wettest Quarter), BIO9 (Mean Temperature of Driest Quarter), BIO11 (Mean Temperature of Coldest Quarter), BIO12 (Annual Precipitation), BIO14 (Precipitation of Driest Month), BIO15 (Precipitation Seasonality); Vegetation Continuous Fields (Hansen et al., 2003); elevation above sea level (Gesch et al., 1999); pastures and croplands (Ramankutty and Foley, 1999). Collinearity among continuous explanatory variables was tested by generating a matrix of pair wise correlations using the Spearman rank correlation coefficient. If two variables were correlated >0.75, the one that explained less in the univariate was excluded from further modeling. Three alternative maximum models were built to allow for the inclusion of the three variables that explained higher deviance in the univariate analyses. Given that the combination of two variables can result in a significant explanation of the response variable even if each variable separately is not informative, all non correlated variables (whether significant in the univariate analysis or not) were included in the multivariate maximum model. To check for collinearity among continuous variables, the categorical variable (land cover), and interactions, we calculated the variance inflation factors (VIFs) (Davis et al., 1986). If any of the VIF values indicated multicolinearity, i.e. VIF >5 (Zuur et al., 2009a), the variable with the highest VIF was dropped, the VIFs were recalculated and the process was repeated until all values were lower than 5. Once the largest set of explanatory variables without collinearity was identified for each of the three models, a backward stepwise manual procedure was performed to evaluate which variables to keep, following the protocol of Zuur et al. (2009b). Decision rules for dropping variables were based on an Akaike's information criterion (AIC, Akaike, 1974), a test comparing the nested models at each step. Models with delta AIC lower than 2 were considered equivalent. To simplify the models, the levels in a factor that were not significantly different were merged together (Nicholls, 1989). This procedure was stopped when the merging implied a significant decrease in total explained deviance (chi^2 test for the change in deviance with 1 df and alpha of 0.01). All final resulting models were bootstrapped to further check the significance of each selected variable. If the confidence intervals of any of the parameter

estimates included the zero value, that variable was removed from the model. To assess the accuracy of the selected models, we calculated the percentage of explained deviance, which is the equivalent of variance in maximum likelihood estimation techniques. All geographical processing was performed with Arcview 3.2 (E.S.R.I., 2000) and statistical analyses with the open-source software R 2.15.1 (R Development Core Team, 2012) with lme4 (Bates et al., 2015) and boot (Canty and Ripley, 2014) packages.

As the modeling resulted in weak models that explained less than 10% of the richness variance, the spatial correlation of species richness was analyzed using semivariograms, which describe how sample data are related with separation distance. It plots lambda, one-half the average squared difference between paired data values, as a function of h, the distance separating the points. When there is spatial dependence the semivariogram increases with h. If it does so without leveling off (unbounded), this indicates the presence of a trend or gradient, which might be due to a gradient in the environment (Jongman et al., 1987). When it levels off, this indicates the presence of autocorrelation, or the tendency of close pairs to be more similar than distant ones. The value of lambda (h) when it levels off is called the "sill" and the corresponding value of h is the "range." The latter represents the maximum distance at which there is spatial dependence and, beyond it, observations become independent. The intercept of the variogram at h = 0, which is zero in ideal conditions, is sometimes higher due to intrinsic variation, sampling error or spatial dependence acting at separations lower than that of the sampling; it is called the "nugget." As the semivariogram is estimated for discrete separation classes (lags), a model needs to be fitted to estimate the values for all h. Standardized semivariograms (lambda/sigma^2) were utilized to describe the spatial structure of species richness. In this type of variogram one unit equals the variance, so the sill would approximate 1 as it estimates the total sample variance. The difference between the sill and nugget represents the proportion of the total variance that can be modeled as spatial dependence (Rossi et al., 1992). We used the robust modification of semivariograms (Cressie, 1993), a lag of 5 km up to 400 km separation distance and a minimum of 30 pairs of points per lag estimate. The semivariogram was fitted by weighted least squares. Analysis was carried out with S-PLUS 6 software (Insightful Corp., 2002). Following the variogram results, we gridded the area with 0.5° cells and recalculated richness at that scale. The new richness data was modeled with GLM as before, but with explanatory variables recalculated at the 50 km grid scale. We considered the median at each cell and for altitude the maximum value in the cell, as well. In order to identify and describe the patterns of small mammal species richness, a richness map was drawn using a grid size of 0.5° and DIVA-GIS software (5.2 version, Hijmans et al., 2005a).

In the second model we used Simpson's diversity index as response variable. This index reflects not only how many species are there in each sample but also how evenly they are distributed (Magurran, 2004). For this model we assumed a gamma distribution of errors and applied the inverse function as link between the response variable and the linear predictor (Nelder and Wedderburn, 1972; McCullagh and Nelder, 1989). In the second model, we used species richness as response variable, assuming poisson distribution of errors and applying the log function as link between the response variable and the linear predictor. Due to we assumed Poisson distribution for residuals, we evaluated overdispersion (Nelder and Wedderburn, 1972; McCullagh and Nelder, 1989; Crawley, 2007). For both models, we chose the explanatory variables among the 49 environmental layers. To select these variables and to avoid collinearity and redundancy, we computed a Spearman's correlation (Zuur et al., 2007). We used a correlation coefficient ≥0.75 to identify highly correlated variables (Rissler

et al., 2006; Martínez and Di Cola, 2011) and we chose the variable among them that we considered more biologically meaningful and easier to interpret. A manual upward stepwise multiple regression procedure was used with alpha ≤0.05 for retention of explanatory variables (Zar, 1999). The addition of explanatory variables into a model was stopped when the variable were not significant. The explanatory power of the model was estimated using ((null deviance − residual deviance)/null deviance)×100, which is equivalent to R^2 in least-square models. The model was checked for normality plotting residuals versus fitted values and by means of Shapiro test (Crawley, 2007). The analyses mentioned above were performed using R (2.15.1 version, R Development Core Team, 2012).

Colonization and loss of species: Changes in small mammal species richness across Patagonia were quantified plotting the actual richness of each one degree latitudinal band, the cumulative colonization (number of species that would have accumulated if no losses had offset the observed colonizations) and the cumulative losses (number of species that would have remained if no colonizations had offset the observed losses; see Brown et al., 2001 for a similar procedure). Thus the number of species per band was counted, using the complete latitudinal bands (i.e., bands from Atlantic Ocean to the Andes) and recording the "gain" or "loss" of different species. These analyses were performed on the basis of distributional maps set up with data from our owl pellet analyses and completed with trapping data (Patton et al., 2015 and the references therein).

3. Results

The initial modeling of richness was poor, although some variables were statistically significant, only 10% of the variance was explained suggesting a doubtful association. Richness varied between 4 and 18 with a variance of 5.41. The standardized variograms showed spatial dependence of richness up to ranges of 50−100 km, depending on the lag used (5 and 10 km respectively, only the 5 km lag variogram is shown in Appendix 4, electronic version only). The resulting nugget of 0.42 λ/σ^2 suggests that 42% of the variance in richness occurs at distances closer than 5 km. The sill of 0.39 λ/σ^2 suggests that 39% of the variance in richness is related to separation up to 50 km. According to these results, a grid size of 50 km was chosen to merge data, due to choosing a grid size of 100 km would be too coarse for the study area.

On the basis of 205 localities and 83,813 individuals quantified (Fig. 1A), 2 marsupials and 21 rodent species were recorded. Among rodents, 3 taxa were caviomorphs and 18 were sigmodontines. The analysis of species richness per grid showed a maximum richness value of 18 and a minimal of 4 (Fig. 1B).

The southern Patagonia, south to Deseado river, is associated to richness values < 13 (MNI = 18,322; N = 48). In clear contrast, the highest values of species richness were located north of Deseado river (MNI = 65,491; N = 157). The lowest values (from 4 to 6) were mostly recorded in the eastern coastal area, independently of latitude. Grids with the highest values (from 16 to 18) were detected in a northwestern fringe of Andean piedmont and in the central-western band around 42°-44°S (Fig. 1B). In a general view, there is a positive agreement between the grid-pattern of richness and the altitudinal variation (Appendix 5, electronic version only).

Spearman's correlation coefficients of environmental variables and richness are shown in Table 1. For the set all localities, species richness was mainly and positively related to longitude and mean temperature of driest quarter; for the set North of Deseado river it was positively related to longitude, while for the set south of Deseado river, six variables were most related to species richness. In this last set, December precipitation and latitude were negatively
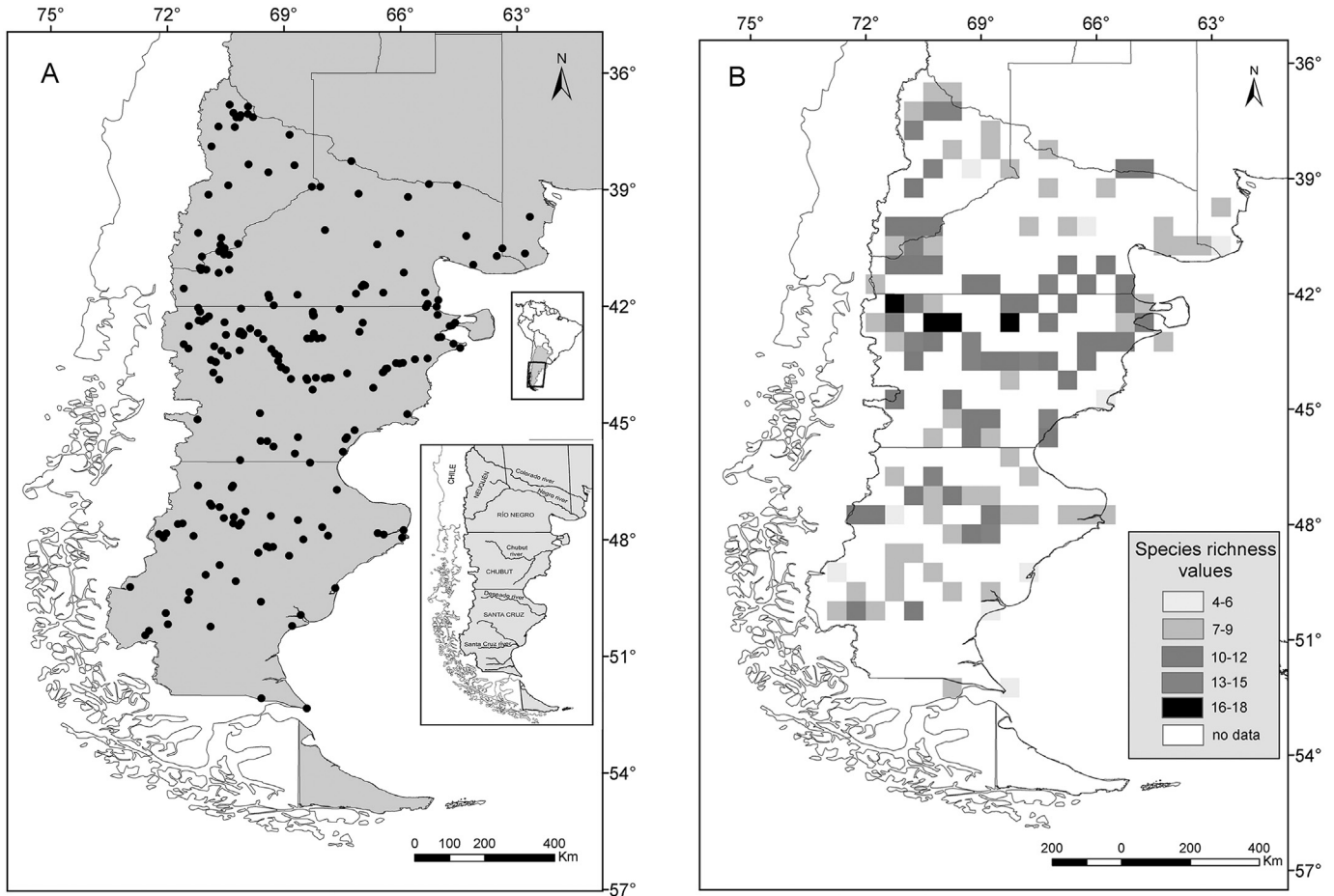
Fig. 1. A) Study area including localities with MNI ≥90 (N = 205). Province and river names are shown in the inset. B) Grid map showing the pattern of small mammal species richness.

related to species richness, while mean temperature of driest quarter, temperature seasonality, mean temperature of warmest quarter and maximum temperature of warmest month were positively related. Although in the grid map (Fig. 1B) there an association between species richness and altitude (Appendix 5, electronic version only), showing low values of richness when altitude is low and higher values of richness when altitude is higher, the correlation coefficient between these variables was low (Table 1). In turn, the generalized linear models showed that this variable could play an important role in modeling the pattern of

Table 1
Spearman's correlation coefficients (r) between environmental variables (16 selected and latitude and longitude) and species richness for the three data set (all localities, localities North of Deseado river and localities South of Deseado river). Variables are alphabetically arranged, highest values are in bold and those significant (p < 0.05) are followed by asterisk.

Variable	All localities	North	South
Altitude	0.15*	0.20*	0.13
Annual precipitation (BIO 12)	0.05	0.09*	−0.27
Cropland	−0.20*	−0.22*	−0.28
December precipitation	−0.28*	−0.27*	**−0.45***
Herbaceous cover	0.01	−0.01	−0.14
Latitude	0.10	−0.14*	**−0.34***
Longitude	**0.34***	**0.29***	0.11
Maximum temperature of warmest month (BIO 5)	0.10	−0.15	**0.32***
Mean temperature of coldest quarter (BIO 11)	−0.03	−0.25*	0.14
Mean temperature of driest quarter (BIO 9)	**0.30***	0.19*	**0.50***
Mean temperature of warmest quarter (BIO 10)	0.05	−0.19*	**0.34***
Mean temperature of wettest quarter (BIO 8)	−0.20*	−0.26*	0.09
Pasture	0.10	0.12*	−0.16
Precipitation of coldest quarter (BIO 19)	0.21*	0.24*	−0.12
Precipitation of driest month (BIO14)	−0.14	−0.14*	−0.28
Precipitation of Wettest Quarter (BIO16)	0.13	0.15	−0.19
Temperature seasonality (BIO 4)	0.08	−0.09*	**0.46***
Tree cover	−0.03	−0.08	−0.19

species richness in Patagonia (see below).

According to the GLM of the clustered results at 50 km spatial cells, the three more explanatory variables in the unvaried analyses were maximum altitude, mean altitude and BIO15 (Precipitation Seasonality). The sets of variables correlated higher than 0.75 were wind and daytime range; BIO1 (Annual Mean Temperature), BIO8 (Mean Temperature of Wettest Quarter) and BIO11 (Mean Temperature of Coldest Quarter); tree cover, BIO12 (Annual Precipitation) and BIO14 (Precipitation of Driest Month); mean and maximum altitude; grass and bare soil cover. The models derived from the maximum model with mean altitude and BIO15 (Precipitation Seasonality) were discarded due to non significance after bootstrapping the parameters. The best two models included maximum altitude, daytime range, BIO9 (Mean Temperature of Driest Quarter), Wet days and the interaction of maximum altitude with daytime range. The difference was that Model 1 included BIO12 (Annual Precipitation) and Model 2 Land use (Appendix 6, electronic version only). The variograms of the residuals of these models showed no spatial dependence (all nugget).

The dynamics of small mammal species richness examined across latitudinal bands (Appendix 7, electronic version only) are shown in Fig. 2 and Appendix 8 (electronic version only), and the small mammal species added to these analyzes are shown in Appendix 9 (electronic version only). The number of species decreased with increasing latitude and species turnover was minimal. The maximum richness (27) was observed in the band 2 (40–41°S) and 10 colonizations were observed southwards. From band 2, species richness decreased, losing between 1 and 5 species per band. In the southernmost band (band 14, Fig. 2 and Appendix 7), the loss of 19 species was recorded, remaining only 8 small mammals species. On the other hand, the geographic range of other species continues southwards reaching the Santa Cruz river (e. g., *Notiomys edwardsii*) or the Magellan Strait (e. g., *Eligmodontia morgani*, *Phyllotis xanthopygus* and *Geoxus michaelseni*).

4. Discussion

The decline in species richness with increasing distance from the tropics is a consistent pattern that has been demonstrated in various taxa and across several continents (see a review in Hawkins et al., 2003). Such macro-scale findings have fascinated biogeographists for decades and hypothesis attempting to explain this diversity pattern are abundant (e.g., Gaston, 2000; Rohde, 1992; Rosenzweig, 1992; Brown, 2014). However, consistent patterns are elusive at smaller spatial scales (e.g., regional or subcontinental

scales), since climatic, environmental and taxon-specific contingencies are likely to interact to modify general richness patterns (Srinivasan et al., 2014). Species richness of non-flying small mammals in Patagonia decreases from northwest to southeast, in general accordance to the global pattern of species richness. A similar situation was observed among bats, whose richness in Patagonia decreases from northwest to southeast, showing a sharp change around 43°S - 46°S (Udrizar Sauthier et al., 2013).

In this work, a main difference was found between northern and southern portions of Patagonia, including high richness values at the north and high correlations between species richness and some environmental variables to the south. In this sense, both historical and climatic factors could be playing a key role in determining the current pattern of Patagonian small mammal species richness:

i) Historical factors such as the glacial cycles that occurred during Pleistocene have promoted the fragmentation and loss of suitable habitats for many species, leading to eventual population fragmentation and subsequent extinction (Pardiñas et al., 2011; Sérsic et al., 2011). Extreme cold temperatures affected most Patagonia, especially in the high altitude areas in the Andes and steppes south of 46°–47° (Rabassa, 2008). High values for species richness at northwestern Patagonia are perhaps the reflection of largest areas of Pleistocene refugia free of ice, where species were sheltered during these weather conditions of glaciations. Phylogeographic patterns based on mtDNA studies are in accordance with this hypothesis, showing that several refugia would have existed on current areas of high small mammal species richness (Cosacov et al., 2010; Sérsic et al., 2011; Pardiñas et al., 2011).

ii) As Kaufman (1995) suggested, abiotic factors are more likely to be limiting in high latitudes and to decrease in importance towards the Equator. As a whole, this could be the case of Patagonia, where small mammal species richness was conditioned mostly by environmental factors south of 46–47°S, at least judging by the results of Spearman's correlations. Extreme physical conditions result in physiological stress, affect fitness, and must be countered by behavioral and physiological adaptations which require expenditure of energy (Kaufman, 1995). According to the variables that we analyzed, we found that temperature, altitude, land cover and annual precipitation are among the factors affecting the pattern of species richness in Patagonia. Our findings contrast with those of Andrade and Monjeau (2014) who generalized that variation in the
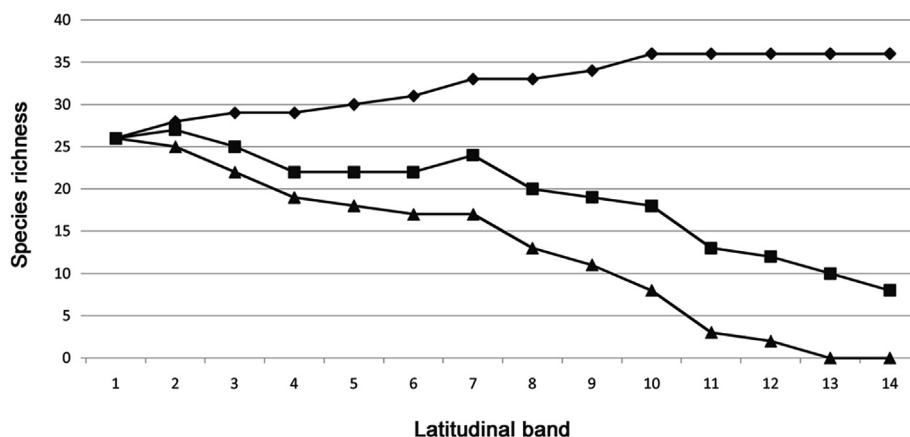

Fig. 2. Dynamics of small mammal species richness. Variation in species richness across latitudinal bands (squares), cumulative colonizations (diamonds) and cumulative losses (triangles).

composition of small mammal assemblages across all Patagonia is mostly driven by temperature.

Despite the hypothesis above mentioned, we cannot set aside the importance of other factors, such as the largest area of northern Patagonia against southern Patagonia or even some "peninsular effect," since at a continental scale, Patagonia can be considered a peninsula. Thus having a larger area, north Patagonia holds more niches and more species than south Patagonia (Simpson, 1964; Taylor and Regal, 1978). In the same way, most of the grids with high values of species richness are located on medium altitude areas of Patagonia (500—1000 m), perhaps as a reflection of the higher habitat heterogeneity of these places compared to the lowland ones (Paruelo et al., 1998b). In fact, the results of the generalized linear models are in line with this.

With increasing latitude, the geographic limit for some species coincides with the course of main rivers. This is the case of species from Pampean region, such as *Akodon azarae* that reaches the Negro river (Río Negro province) and does not get over it (Pardiñas, 2009) and *Holochilus brasiliensis* that barely surpass the limit of Colorado river (Buenos Aires province; Formoso et al., 2010). Species apparently associated to the shrubby environments of the Monte P.P. reach their southern limit at the Deseado river (Santa Cruz province), as in the case of *Akodon iniscatus* (Pardiñas, 2009), *Eligmodontia typus* (Da Silva, 2011), *Galea leucoblephara* (Agnolin et al., 2008), *Graomys griseoflavus* (Udrizar Sauthier et al., 2011) or *Thylamys pallidior* (Formoso et al., 2011). For *Calomys musculinus* (de Tommaso et al., 2014) and *Notiomys edwardsii* (Pardiñas et al., 2008) the limit of their geographic distribution seems to be in the Santa Cruz river. It is tempting to suggest a causal relationship between the distributions of these small mammals and major rivers acting as geographic barriers.

Most of the observed latitudinal decrease in species richness occurs by loosing different taxa, almost without turnover in the small mammal assemblages (i.e., each species reaches a southern latitude in its geographic distribution and do not continue further [Fig. 2]). This result contrasts with that found for several taxa, including small rodents, in high latitude areas of the Northern Hemisphere, where it was observed that mammal diversity reflects high species turnover between middle and high latitudes (e.g., Baquero and Tellería, 2001; Brown et al., 2001; Svenning et al., 2011). In addition, postglacial recolonization of high latitude regions of Northern Hemisphere occurred from low latitude refugia in a wide range of taxa (Lessa et al., 2003), contrasting with the situation of the southern Patagonian biota that have had little biological input from lower latitudes (Fraser et al., 2012). These trenchant differences between Northern and Southern hemispheres can be linked with the strongly contrasting distribution and extension of the main ice sheets during glacial times (Ehlers and Gibbard, 2004). Based on the study of several groups of vertebrates, Sérsic et al. (2011) suggested that most of the glacial refugia occurred in Patagonia North of 46—47° S. Southern colonization from northern areas was suggested for various taxa, whose high latitude populations are currently under an scenario of demographic expansion (e.g., *Abrothrix hirta, Loxodontomys micropus*; Sierra, 2010; Cañón et al., 2010; Teta and Pardiñas, 2014). Available evidences suggest that southern colonization of Patagonia occurred along the Pleistocene, following the cycles of expansion-retractions of the glaciers (Lessa et al., 2010). Within this context, the differential (or lack of) phylogeographic breaks between species (Cañón et al., 2010; Lessa et al., 2010; Sierra, 2010; Alarcón et al., 2011; Pardiñas et al., 2011) are in accordance with species specific responses to changing climatic conditions.

Taken the evidence as a whole, we suggest that current species richness distribution in Patagonia is the result of historical (glacial history and main rivers acting as geographic barriers) and current climatic factors along with species ecology (partially evidenced by different demographic histories and dispersion capabilities). This pattern is better expressed at southern latitudes (46—47° S) as this part of Patagonia combined a major pressure of climatic conditions (with a strong influence of glaciations during the Pleistocene; Rabassa, 2008). These results are in agreement with those of other authors suggesting that in those areas historically impacted by glaciers, selective colonization and extinctions seem to determine current species distribution patterns (Taberlet et al., 1998; Araujo et al., 2008; Fløjgaard et al., 2011; Srinivasan et al., 2014). In addition, our results highlight the importance of northern Patagonia as a reservoir of diversity across time. Moreover, as most of the glacial refuges were potentially located on this area, we might expect it to be more severely impacted by current global warming, an issue that is needed of further address.

Acknowledgements

Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.jaridenv.2016.07.007.

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