



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 km² (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 abiotic than biotic 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 Subantarctic 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 through 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

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