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Journal of Mammalian Evolution

ISSN 1064-7554

J Mammal Evol
DOI 10.1007/s10914-020-09497-7

Springer

Journal of Mammalian Evolution
https://doi.org/10.1007/s10914-020-09497-7

ORIGINAL PAPER

An Ecomorphological Comparative Study of Extant and Late Holocene Sigmodontinae (Rodentia, Cricetidae) Assemblages from Central-Eastern Argentina

Sofía Barbero[1,2] · **Pablo Teta**[1,2] · **Guillermo H. Cassini**[1,2,3]

Abstract

The anthropic effect associated with worldwide European settlements over the last 500 years has caused dramatic environmental changes, modified regional patterns of biodiversity, and often led to local or complete extinctions. The sigmodontine rodents of Bahía Samborombón (Humid Pampas, central-eastern Argentina) constitute a good case study: a late Holocene archaeological site allowed us to compare a pre-European settlement assemblage (12 species) with the extant one (nine species). We used linear morphometrics (16 cranial and ten mandibular measurements) to assess interspecific morphological variations of the masticatory apparatus in relation to dietary habits for each assemblage. Even though sigmodontines have a tendency towards omnivory, groups based on dietary preference only overlapped partially. Size was one of the main variables involved in niche segregation, and shape characteristics such as rostrum elongation or mandible robustness were linked to different diets. We found that a combination of dietary preference and size was associated with extinctions. The main morphospace change between the two assemblages was related to the local extinction of the three greater insectivores and the smallest graminivore, located towards the center of the assemblage's morphospace. An insectivore was incorporated, involving no significant changes in the general morphospace. Graminivores and larvivores were not affected. Our study sheds light on the causes of local extinctions of small mammals at the Humid Pampas, a phenomenon that had never been studied from an ecomorphological approach.

Keywords Anthropic effect · Rodents · Cricetid · Ecomorphology · Local extinction · Pampa

Introduction

Dramatic landscape changes, primarily due to anthropic activities, took place worldwide during the Holocene, and especially over the last 500 years (MacPhee and Flemming 1999; Turvey 2009). Such activities led to local and complete extinctions, to the extent where virtually all of the species and population losses from this time can be interpreted as human-caused events (Turvey and Fritz 2011). This period was characterized by the settling of European colonists around the globe, and the expansion and consolidation of mercantilist European colonies in South America (Céspedes del Castillo 2009). In this scenario, regional patterns of biodiversity were altered through disturbance of natural environments, overexploitation of resources, and introduction of species (e.g., Steadman and Martin 2003; Turvey and Fritz 2011). Disruption of ecosystems is known to lead to richness reduction through dominance of opportunistic species at the expense of the loss of the most specialized taxa, which would be unable to quickly adapt to changing environments (Gray 1989; McKinney and Lockwood 1999; Devictor et al. 2008). The impact of the European settlements around the world resulted in the extinction of between 40 and 100 species of mammals (depending on the estimation), with Rodentia the mammalian order that lost the most species (up to 43)

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s10914-020-09497-7) contains supplementary material, which is available to authorized users.

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(MacPhee and Flemming 1999). In continental South America, at least one marsupial, one bat, and up to seven rodents were lost in the last 500 years (Turvey 2009; Teta et al. 2014). In the Humid Pampas, central-eastern Argentina (sensu Olson et al. 2001), landscape modifications were mediated mainly by sheep, cattle, and crops (Bilenca et al. 2007). As expected, the use of land for ranching and farming caused habitat uniformity (Paruelo et al. 2005), which benefited opportunistic taxa, leading to their dispersion and population increase. This, in turn, implied significant range retractions and variations in the abundance of the populations of other taxa, sometimes provoking local extinctions over hundreds or thousands of kilometers (Pardiñas 1999; Teta et al. 2014). Accordingly, the extant configuration of mammalian assemblages in this region is believed to have been generated after the settling of Europeans. Even though anthropic effect and recent extinctions have been studied for the Humid Pampas (e.g., Teta et al. 2014), they were never assessed with an ecomorphological approach, not even for rodents, the most impacted order.

Ecomorphology studies morphological variation of organisms and its interaction with their ecology, allowing researchers to answer questions such as how an organism's skull morphology is related to its diet (Van Der Klaauw 1948; Bock 1990; Liem 1991; Wainwright and Reilly 1994; Motta et al. 1995; Norton et al. 1995; Cassini et al. 2011; Vizcaíno et al. 2011, 2016; Kraatz et al. 2015; Thorpe 2016; Benson et al. 2017; Forrest et al. 2018; Law et al. 2018). It is useful to reconstruct the functional diversity of paleocommunities, as well as to understand extant ones, and changes that led from one to the other (e.g., Spencer 1995; Cassini 2013; Price and Schmitz 2016). Ecomorphological studies are a fundamental tool to understand regulation of biodiversity through an insight into the complex interaction between organisms and modifications of their environment (Price and Schmitz 2016). Therefore, they constitute a good approach to study the impact of human-caused changes on biodiversity. Regarding functional morphology and diet, ecomorphology's premise is that coexistence of several species in a community implies differential use of feeding resources as a base for niche differentiation (Hirst 1975; Jarman and Sinclair 1979; McNaughton and Georgiadis 1986). The role of size is proposed to be significant in niche partitioning (e.g., Jarman 1974; Bodmer 1989; Vizcaíno 2000; Vizcaíno et al. 2004, 2011; Cassini et al. 2012), and, when size differences are not prominent or several taxa with the same size are overlapping, then evidence aims at morphological variation independent of size. Morphometric variables have been related to diet in multiple studies for different orders of mammals in diverse assemblages (see Van Valkenburgh 1994; Morales and Giannini 2013; Schiaffini and Prevosti 2014 for Carnivora; Spencer 1995; Mendoza and Palmqvist 2006; Cassini et al. 2011, 2012; Giannini and García-López 2014 for different ungulate orders; De Esteban-Trivigno 2011; Vizcaíno et al. 2011 for cingulates). As for rodents, while some approximations exist, they are general (Samuels 2009; Maestri et al. 2016b) or focused only on certain taxonomic groups, such as Caviomorpha (Verzi and Olivares 2006; Álvarez et al. 2011, 2015) or Ctenomyidae (Morgan et al. 2017). Sigmodontinae rodents, on the contrary, constitute a group practically unexplored from this perspective. Although morphology and diet are documented for several species (e.g., Ellis et al. 1998; Suárez and Bonaventura 2001; Villafañe et al. 2005; Dellafiore and Polop 2010), we are not aware of a transversal study involving a detailed analysis of them and their functional relationships.

Sigmodontinae (Rodentia, Cricetidae) is a highly diverse family of rodents, comprehending about 434 extant species distributed in 87 genera (Patton et al. 2015; Pardiñas et al. 2017a). They are endemic to South, Central, and North America, with most species occurring in the Neotropical region, where they are represented in environments ranging from tropical forests, woodlands, meadows, and wetlands to salt marshes, steppes, and deserts (Patton et al. 2015). As fundamental elements of the Neotropical mammalian fauna, they play a central role in the trophic chains of practically all of its terrestrial environments (Patterson 1999). The dietary habits of sigmodontines range from animalivorous species (e.g., *Oxymycterus rufus, Scapteromys aquaticus*) to strictly herbivorous ones (e.g., *Reithrodon auritus, Holochilus vulpinus*). Preference, availability, and quality of food items have been presented as the most determining factors structuring an assemblage (Dellafiore and Polop 2010).

Distribution and biogeography of sigmodontine rodent assemblages (sensu Stroud et al. 2015) at the Humid Pampas were studied by Pardiñas et al. (2010a, b). The assemblage found in the area surrounding Bahía Samborombón (central-eastern Argentina) is comprised of nine species: *Akodon azarae, Calomys laucha, C. musculinus, Deltamys kempi, Holochilus vulpinus, Oligoryzomys flavescens, Oxymycterus rufus, Reithrodon auritus,* and *Scapteromys aquaticus* (Table 1) (Teta et al. 2013). The extant landscape is characterized by a mosaic of grasslands, wetlands, swamps, and salt marshes (Fernández et al. 2004). Paleontological and palynological evidence suggests that grasslands have dominated this region since at least the Neogene (Prieto 2000); however, transformations associated with anthropic activities have been registered for this area for the last five centuries (e.g., Rapoport 1996; Zalba and Villamil 2002; Alberio and Comparatore 2014). Its use for pasture and farming has introduced exotic grasses and forbs, changing the composition of the grasslands (Hannah et al. 1995; Miñarro and Bilenca 2008). Natural grasslands, among the ecosystems most disturbed by humans, may have been modified to the point of no return (Ghersa et al. 2002; Alberio and Comparatore 2014). As a result, local extinctions of various vertebrates have been

Table 1 Sigmodontine species present in the strip of coastal wetland of Bahía Samborombón, in the late Holocene and extant assemblages

Species	Common name	Holocenic	Extant	*Average body mass* (gr.)	*Dietary category*	*n*
Akodon azarae	Azara's grass mouse	X	X	$24^{a,c}$	Insectivore	20
Bibimys torresi	Torres's crimson-nosed rat	X		28^{c}	Insectivore	4
Calomys laucha	Small vesper mouse	X	X	14^{c}	Granivore	20
Calomys musculinus	Drylands vesper mouse	X	X	20^{c}	Granivore	20
Deltamys kempi	Kemp's akodont		X	24^{a}	Insectivore	12
Holochilus vulpinus	Web-footed marsh rat	X	X	326^{b}	Graminivore	20
Necromys lasiurus	Hairy-tailed bolo mouse	X		31^{b}	Insectivore	20
Necromys obscurus	Dark-furred akodont	X		43^{b}	Insectivore	13
Oligoryzomys flavescens	Yellow pygmy rice rat	X	X	21^{c}	Granivore	20
Oxymycterus rufus	Red hocicudo	X	X	76^{b}	Larvivore	20
Pseudoryzomys simplex	Brazilian false rice rat	X		42^{a}	Graminivore	7
Reithrodon auritus	Bunny rat	X	X	80^{a}	Graminivore	18
Scapteromys aquaticus	Argentine swamp rat	X	X	112^{b}	Larvivore	20

Presence is indicated with an X. Body mass data are from a. Pardiñas et al. (2017b), b. Leveau et al. (2006), and c. Maestri et al. (2016a). *n* indicates the number of specimens measured for each species.

documented in the area, for example, several bird species (Azpiroz et al. 2012) and, among mammals, the large felids *Panthera onca* (jaguar) and *Puma concolor* (puma) and the cervid *Ozotoceros bezoarticus* (pampas deer) (Soriano et al. 1991; Miñarro and Bilenca 2008).

The effect of habitat modification on sigmodontine rodents can be assessed through the comparison of late Holocene and extant assemblages (examples for other mammals can be found in Tonni et al. 1999; Pardiñas and Tonni 2000). It is possible to compare the assemblage found in the Bahía Samborombón area about 500 years ago (12 species) and in the present (nine species) thanks to data from the archaeological site "El Divisadero Monte 6" (Teta et al. 2013). Briefly, these authors documented a reduction in species richness and diversity. Even though this constitutes a good first approach to the issue of the effect of anthropic changes on sigmodontine assemblages, it could be enriched by incorporating an analysis of how form and function affected extinction and survival of species in this assemblage.

Rodents'generalized craniomandibular morphology is related to their specialization towards gnawing. Their skull has an elongated rostrum and hypsodont incisors, canines are absent, and their long diastema is followed directly by two or more pairs of molars. An expanded glenoid fossa allows rodents' jaws to perform two distinct functions: gnawing and grinding. The masseter is large, constituting the main muscle used in these processes (Kay and Hoekstra 2008; Samuels 2009; Druzinsky 2015). Despite their general body plan being relatively conserved, an array of possible adaptations for different dietary strategies is presented throughout rodent species, with variations in traits such as skull shape, occlusal morphology, and masseter muscle structure (Samuels 2009; Hautier et al. 2012). Sigmodontine rodents in particular present a configuration of the masseter considered to be a compromise between the opposing strategies of gnawing and grinding. This results in their craniomandibular morphology showing a generalist phenotype, highly successful at exploiting different dietary niches (Maestri et al. 2016a).

In this study, we made an ecomorphological comparison of the masticatory apparatus of sigmodontine rodents present in the late Holocene archaeological site "El Divisadero Monte 6" and the extant assemblage in the area surrounding it. Our objective was to characterize the morphospace occupied by the sigmodontine species of the late Holocene and extant assemblages from Bahía Samborombón. Our hypothesis was that anthropization of this region throughout the last 500 years modified the sigmodontine assemblage, reducing the total morphospace occupied. As diet is one of the primary factors affecting niche partitioning, modifications on the morphospace of diet-related skeletal traits could indirectly inform us of changes in the niches occupied by sigmodontine rodents.

Methods

Study Area

The study area was the strip of coastal wetland of Bahía Samborombón, central-eastern Argentina (Fig. 1), where the Depressed Pampas and the Tala District converge (Cabrera 1968). The Depressed Pampas are characterized by flat to undulating relief, with periodical floods and droughts. Their climate is subhumid with mesothermic features regulated by the tempering effect of the Atlantic Ocean (mean annual temperature ranges from 10 to 20 °C), and with an annual rainfall between 400 and 1600 mm (Burgos 1968; Soriano et al. 1991). The Tala district consists of xerophilic vegetation (*Celtis spinosa*, *Jordina rhombifolia,* and *Acacia caven*) rooted in sandy lowlands alongside rivers (Cabrera 1968). The coastal wetlands in particular have daily marine tides, which structure the landscape with salt marshes and grasslands (Fernández et al. 2004). Typical local plant communities include *Bothriochloa laguroides*, *Paspalum dilatatum,* and *Briza subaristata*. Currently, depending on the timing and length of the flooding period and soil salinity, grassland or plant communities characteristic of flooded areas are developed there.

Within this area there is an archaeological site from the late Holocene: "El Divisadero Monte 6" (Teta et al. 2013). It is located in the county of General Lavalle (ca. 36°23' S y 56°56'W), by the stream Las Tijeras, inside a dense stand of *Celtis tala*, on a smooth hill around 2 m above sea level. This site's age was estimated by radiocarbon dating in 540 ± 60 rcybp (LP1687), and 510 ± 50 rcybp (LP- 3178) (Vázquez 2017). Several sigmodontine rodent specimens were found there, associated with predation by birds of prey and, to a lesser extent, with anthropic consumption.

Late Holocene and Extant Assemblages

We followed Teta et al. (2013) for the species composition of both the late Holocene and extant assemblages. These were based on sigmodontine skulls recovered from owl pellets. The pellets were from the site "El Divisadero Monte 6" for the late Holocene assemblage, and from the following localities in the surrounding area for the extant assemblage: Puesto El Plátano (36°10' S, 57°24' W), Mar del Tuyú (36°34' S, 56°41' W), and General Madariaga (36°59' S, 57°08' W) (Table 1; Fig. 1).

Specimens

We measured a total of 214 mice, representing the 13 sigmodontine species (following Patton et al. 2015) of both late Holocene and extant assemblages. The specimens were housed in the mammal collections at Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN, Ciudad Autónoma de Buenos Aires, Argentina), Fundación de Historia Natural "Félix Azara" (FHNFA, Ciudad Autónoma de Buenos Aires, Argentina), and Museo de La Plata (MLP, La Plata, Buenos Aires Province, Argentina). We selected only those individuals with emerged molars, excluding very young and old adult specimens (e.g., Pearson et al. 1987; Myers 1989). The sample was composed mainly of specimens from the southeastern region of the Buenos Aires Province; however, in order to reach an adequate sample size (i.e., $n \geq 20$) for each species, in some cases we also included animals from the Delta region, the north and the southwestern region of the Buenos

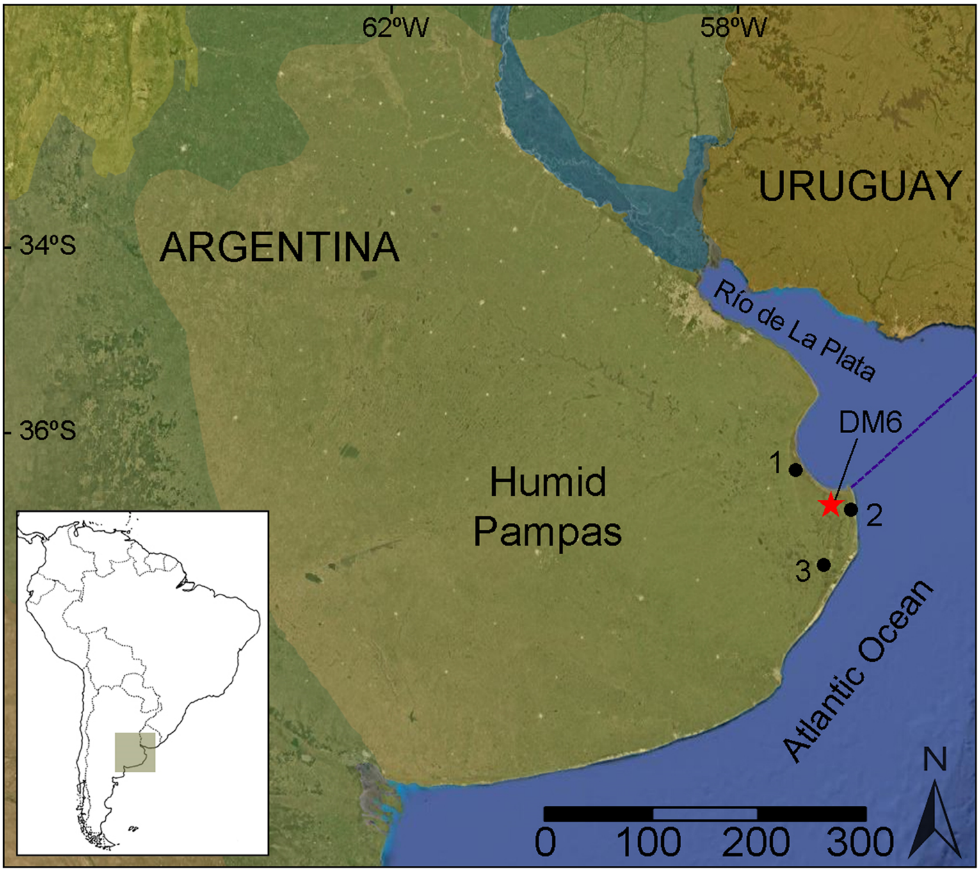

Fig. 1 Map of the Humid Pampas detailing the study area. The star point indicates the archaeological site "El Divisadero Monte 6," and numbers identify localities from which the extant assemblage composition was compiled. 1: Puesto El Plátano, 2: Mar del Tuyú, 3: General Madariaga

Aires Province, as well as northern Patagonia. Given the fragmentary nature of the late Holocene specimens, we were unable to measure those collected at the archaeological site. Under the assumption that they have not undergone significant morphological evolution in the last 600 years, we used the same individuals for the species shared between both assemblages. Regarding the locally extinct species, we used specimens of *Pseudoryzomys simplex* from the Chaco Province and *Bibimys torresi* from northeastern Buenos Aires Province. Some specimens were damaged and had some missing measurements; so, in order to achieve an adequate sample, we estimated the missing data performing a Bayesian Principal Component Analysis (BPCA; see Arbour and Brown 2014; Fernández Blanco et al. 2018) as described by Oba et al. (2003), using the 'pca' wrapper function from the pcaMethods package Version 1.58.0 in R (Stacklies et al. 2007).

Measurements

We took 16 cranial and ten mandibular measurements with an INSIZE 1137–150 digital caliper. The measurements were aimed at describing functional compromises related to food intake and processing, and included length, width, and height of several anatomical traits (Fig. 2) (Musser et al. 1998; Schulze et al. 2003; Geise et al. 2005; Libardi and Percequillo 2016). The following measurements were performed on the skull: braincase breadth (BCB): widest breadth of the braincase, taken between the temporal bones; breadth across the masseteric tubercle (BAMT): ventral breadth of the rostrum between the lingual edges of the masseteric tubercles, at the base of the zygomatic plates; breadth of the bony palate at the first molar (BBPM1): breadth of the bony palate measured at the medium point of the second cuspid of M1, on the external edges of the alveoli; breadth of the bony palate at the third molar (BBPM3): breadth of the bony palate measured at the medium point of M3, on the external edges of the alveoli; condyle-incisive (CI): length of the skull measured from the anterior end of the incisor alveolus to the posterior end of the occipital condyle; infraorbital foramina height (IFH): dorsoventral width of the infraorbital foramen, measured between the ventral edge of the superior root of the zygomatic arch to the rostro-ventral edge of the zygomatic plate; incisive foramina length (IFL): length of the incisive foramen, measured from its anterior to its posterior end; least intraorbital breadth (LIOB): dorsal breadth of the intraorbital region, considering the narrowest distance between the frontal bones; orbital interior length (OIL): length of the orbital region, measured from the posterior end of the zygomatic plate to the anterior edge of the glenoid cavity; palatal bridge (PB): length of the bony palate, measured from the posterior end of the incisive foramina to the anterior end of the mesopterygoid pit; post-palatal length (PPL): distance between the bony palate and the foramen magnum, measured from the anterior edge of the mesopterygoid pit to the anterior edge of the foramen magnum; rostrum length (RL): length of the rostrum, measured from the posterior end of the zygomatic notch to the anterior end of the nasal bone; upper diastema length (UDL): length of the upper diastema, measured from the posterior end of the incisor alveolus to the anterior end of the first molar alveolus; upper molar row length (UMRL): length of the upper molar row, considered from the anterior end of the first molar alveolus to the posterior end of the last molar alveolus; zygomatic breadth (ZB): major breadth between the exterior edges of zygomatic arches; zygomatic plate breadth (ZPB): breadth of the zygomatic plate on its medium portion. The following measurements were performed on the mandible: articular condyle breadth (ACB): breadth of the articular condyle measured on its broader part, from the labial to the lingual side; coronoid heigth (CH): height of the coronoid process, measured from the retromolar pit, on the caudal end of the third molar, to the anterior end of the coronoid process; lower

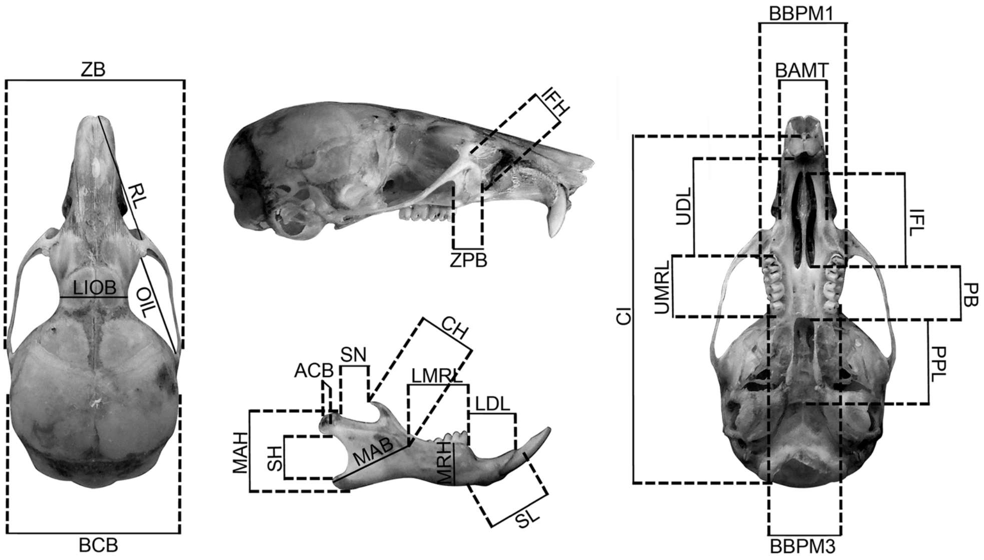

Fig. 2 Craniomandibular measurements used in this study illustrated on a skull of *Abrothrix hirta* (CNP2339, from the mammalogy collection of Centro Nacional Patagónico, Puerto Madryn, Chubut, Argentina)

diastema length (LDL): length of the lower diastema, from the posterior end of the incisor alveolus to the anterior end of the first molar alveolus, measured on the labial side of the mandible; lower molar row length (LMRL): length of the lower molar row, considered from the anterior end of the first molar alveolus to the posterior end of the last molar alveolus; mandibular angle breadth (MAB): from the retromolar pit, on the caudal end of the third molar, to the posterior end of the angular process; mandibular angle height (MAH): from the superior end of the articular condyle to the inferior end of the mandibular angle; mandibular ramus height (MRH): height of the mandibular ramus measured from the labial edge of the first molar alveolus, underneath the second cuspid, vertically to the lower edge of the mandible; semilunar height (SH): height of the semilunar notch, considered from the distal end of the angular process to the inferior end of the condylar process; sigmoid notch (SN): length of the sigmoid notch, measured from the posterior end of the coronoid process to the anterior end of the condylar process measured on the lingual side of the mandible; symphysis length (SL): length of the mandibular symphysis, considered from the anterior end of the incisor alveolus to the inferior end of the mandibular symphysis, measured on the lingual side of the mandible. For size-dependent assessments, variables were base 10 log-transformed previously to the analyses. In addition, we divided each variable by the geometric mean to convert them in shape variables (Mosimann 1970), which were also base 10 log-transformed.

Diet

Information on feeding ecology across different sigmodontine rodents was obtained from the available literature (e.g., Ellis et al. 1998; González and Pardiñas 2002; Villafañe et al. 2005; Dellafiore and Polop 2010). The dietary types were classified using the same system as Kerley and Whitford (1994), which distinguishes between animals on the basis of their diet consisting of ≥50% of the same element. Following Olsen's (2017) procedures, unmatched data were averaged. Four broad dietary categories were defined from a combination of taxonomic identity and mechanical properties of the food (Lucas 2004) as follows: (1) granivores, comprising species whose main dietary element are seeds; (2) graminivores, including those species which primarily consume Poaceae leaf material; (3) insectivores, covering species with a preference for hard shell arthropods; and (4) larvivores, for those species that feed mainly on arthropod larvae and annelids (Table 1).

Morphometric Analyses

We used Principal Component Analysis (PCA) obtained from the covariance matrix to identify the main sources of variation in skulls. We analyzed both the size dependent and shape variable PCAs. To assess the variation in morphological diversity related to ecological traits in both the late Holocene and extant assemblages, we performed the PCAs using the princomp function on R 3.4.0 (R Core Team 2017) with the variables transformed to base 10 logarithms. To assess the morphological disparity between both assemblages, we delimited the morphospace occupied by each dietary group and, subsequently, compared the late Holocene and extant assemblage morphospace. The datasets generated and analyzed during the current study are available from the corresponding author on reasonable request.

Results

The PCAs for both the late Holocene and extant assemblages resulted in about 80% of the variation being explained by PC1 (late Holocene assemblage: 81.83%, extant assemblage: 83.68%). All the variables correlated negatively with this component, and therefore with overall skull size. The PC1 loadings of each variable were very similar for both assemblages, of which SN, PB, LMRL, and MAB were the highest (−0.26 to −0.23) and LIOB was the least explanatory variable (−0.10). PC2 accounted for only about 6% of the variance in both assemblages. Ten variables were negatively correlated with it, of which four had the most negative contributions: SN (late Holocene: −0.42; extant: −0.37), ACB (−0.30), ZPB and SL (~ − 0.23). The remaining 16 variables were positively correlated, with the highest LIOB (~0.35), RL, PPL, and BAMT (0.31 to 0.26) (see Online Resource 1). PC2 in both assemblages was related to more robust skulls and mandibles, with a greater lever arm for the temporalis muscle towards the negative values, and more gracile skulls with more elongated rostra towards the positive values. The morphospace depicted by these two components for the late Holocene assemblage (Fig. 3a) showed partial segregation of dietary groups. It clustered larvivore species (*Scapteromys aquaticus* and *Oxymycterus rufus*) mainly in the second quadrant, graminivore species (*Holochilus vulpinus*, *Pseudoryzomys simplex,* and *Reithrodon auritus*) mainly in the third, granivore species (*Calomys musculinus, Calomys laucha,* and *Oligoryzomys flavescens*) in the fourth, and insectivore species around the origin, with *Necromys obscurus* towards the third quadrant, overlapping partially with the graminivore morphospace, *Necromys lasiurus* between the fourth and first quadrants, and *Akodon azarae* and *Bibimys torresi* in the first.

The comparison between the late Holocene and extant assemblages revealed changes in the morphospace occupied by some species. The species from the late Holocene assemblage that were located in the area surrounding the origin (the greater insectivores *Necromys lasiurus, Necromys obscurus,* and *Bibimys torresi,* and the smallest graminivore *Pseudoryzomys simplex*) were locally extinct. A new species was incorporated in the extant assemblage (the small insectivore *Deltamys kempi*); however, it overlapped almost completely with the

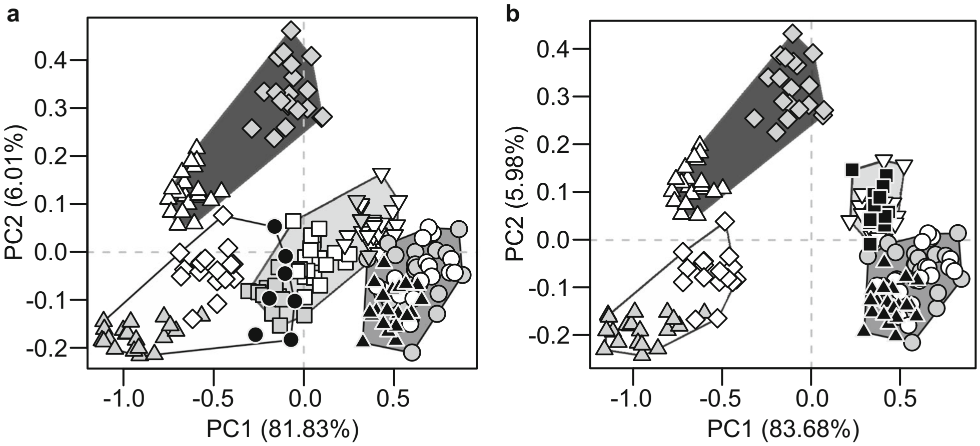

Fig. 3 PCA of the late Holocene (**a**) and extant (**b**) assemblages. Polygons represent diets: white: graminivores; black: larvivores; light grey: insectivores; dark grey: granivores. Symbols represent species: *Akodon azarae*: white inverted triangle; *Bibimys torresi*: grey inverted triangle; *Calomys laucha*: grey circle; *Calomys musculinus*: white circle; *Deltamys kempi*: black square with grey border; *Holochilus vulpinus*: grey triangle; *Necromys lasiurus*: white square; *Necromys obscurus*: grey square; *Oligoryzomys flavescens*: black triangle with grey border; *Oxymycterus rufus*: grey diamond; *Pseudoryzomys simplex*: black circle with grey border; *Reithrodon auritus*: white diamond; *Scapteromys aquaticus*: white triangle

morphospace covered in the first quadrant by one of the remaining species (*Akodon azarae*). Consequently, the addition of this novelty species did not account for any regain of the space lost due to local extinctions. Therefore, although the overall disparity (extreme regions of morphospace) seems to be unchanged, there was a loss in the total morphospace area occupied. Moreover, this lack of coverage of the region around the origin resulted in a complete segregation of dietary groups for the extant assemblage.

Analyses of base 10 log-transformed shape variables (Mosimann variables; i.e., removing the effect of size) resulted in the first eight components accounting for about 85% of the variance for both assemblages (Fig. 4). PC1 explained about a third of the total variation (late Holocene assemblage: 34.89%, extant assemblage: 38.51%). The PC1 loadings for both assemblages showed certain degrees of similarity (see Online Resource 1). Fourteen variables fell under negative values for the late Holocene assemblage, and fifteen for the extant one; LIOB was the highest (~ − 0.42), followed by BAMT, PPL, RL, and IFL (−0.29 to −0.18). The remaining variables fell under positive values, with SN the most explanatory (late Holocene: 0.48, extant: 0.43), followed by SL, PB, ACB, and MRH (0.27 to 0.21). For both assemblages, towards the negative values the PC1 was related to more gracile skulls with greater development of the masseter muscle and wider palates, which could be associated with the masticatory requirements of a graminivore diet. On the other hand, towards positive values PC1 was related to taller and more robust mandibles and skulls, with the molar series closer to the pivot and a greater lever arm for the temporalis muscle, which could be linked to the mechanical stress required by a granivore diet. PC2 explained over 15% of the variability (late Holocene assemblage: 18.66, extant: 16.13), which, added to PC1, comprised more than 50% of it. The most explanatory variables for this component were shared between the late Holocene and extant assemblages. The remaining ones, though varying sometimes in order and individual loadings, showed an acceptable degree of consistency for both assemblages. Under negative values, SN was the most explanatory variable (~ − 0.77). This loading was considerably higher than the rest of the negative ones; thus we consider SN to be governing the variation on this side of the axis. In the late Holocene assemblage, the variables that followed were LIOB, BAMT, PPL, and IFL (−0.16 to −0.09), and in the extant one they were LMRL, IFL, SH, and RL (−0.13 to −0.11). On the other hand, positive loadings were more regular, with no variables clearly dominating the others: CH had the greatest correlation (late Holocene: 0.29, extant: 0.37), with the following variables being SL, ACB, PB, and IFH (0.25 to 0.16) for the late Holocene assemblage and ZPB, ACB, SL, and IFL (0.23 to 0.17) for the extant one (see Online Resource 1). With respect to anatomical traits correlated to this component, negative values would be associated with a greater lever arm for the temporalis muscle, while positive values would be associated with larger attachment areas for the masseter muscle.

The morphospace depicted by the first two components for the late Holocene assemblage (Fig. 4a) showed partial segregation of dietary groups. Graminivore species (*Holochilus vulpinus*, *Pseudoryzomys simplex,* and *Reithrodon auritus*) were clustered mainly in the first quadrant, though reaching the fourth; they overlapped partially with granivore species (*Calomys musculinus, Calomys laucha,* and *Oligoryzomys flavescens*), which were located in the area surrounding the

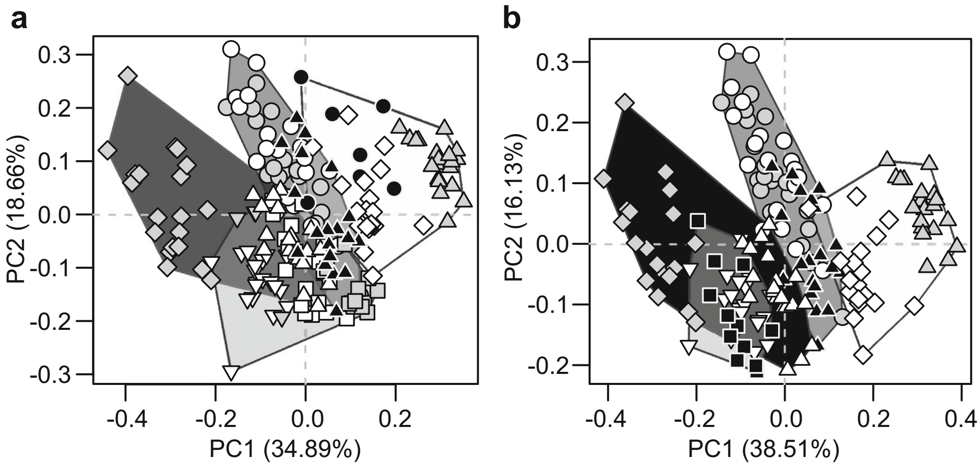

Fig. 4 PCA removing the effect of size of the late Holocene (**a**) and extant (b) assemblages. Polygons represent diets: white: graminivores, black: larvivores; light grey: insectivores; dark grey: granivores. Symbols represent species: *Akodon azarae*: white inverted triangle; *Bibimys torresi*: grey inverted triangle; *Calomys laucha*: grey circle; *Calomys musculinus*: white circle; *Deltamys kempi*: black squarewith grey border; *Holochilus vulpinus*: grey triangle; *Necromys lasiurus:* white square; *Necromys obscurus*: grey square; *Oligoryzomys flavescens*: black triangle with grey border; *Oxymycterus rufus*: grey diamond; *Pseudoryzomys simplex*: black circle with grey border; *Reithrodon auritus*: white diamond; *Scapteromys aquaticus*: white triangle

origin, projecting mainly towards the second and fourth quadrants. Larvivore species (*Scapteromys aquaticus* and *Oxymycterus rufus*) covered a large area in the second and third quadrants, with a minor extension on the fourth. Finally, the area corresponding to insectivore species (*Akodon azarae*, *Bibimys torresi, Necromys lasiurus,* and *Necromys obscurus*) was located mainly over the third and fourth quadrants, though it also reached the second. Changes in the morphospace between the late Holocene and extant assemblage were less apparent in this analysis than in the PCAs with size. The area covered in the late Holocene assemblage by insectivore species that went locally extinct (*Bibimys torresi*, *Necromys lasiurus,* and *Necromys obscurus*) was overlapping in most of its extension with areas occupied by larvivores and granivores. Thus, their absence in the extant assemblage is not accompanied by a significant reduction in the total morphospace covered by the assemblage. Moreover, the novelty insectivore species *Deltamys kempi* overlapped with the area covered by *Akodon azarae*, consistently with the observation of the PCAs with size. Regarding the graminivore species *Pseudoryzomys simplex*, most of its area overlapped either with the surviving graminivore *Reithrodon auritus* or with the area covered by granivores. Consequently, its loss implied only a small change in the total area covered by the assemblage. In plots constructed with the Mosimann variables, the shape PCAs, different dietary groups, and often several different species occupied overlapping areas of the morphospace. Accordingly, composition changes between the late Holocene and the extant assemblage did not result in this case in significant changes of the total morphospace covered.

Discussion

In the present work, we assessed the effect of habitat modification on sigmodontine rodents by morphologically characterizing and comparing a late Holocene and an extant assemblage from central-eastern Argentina (the area of Bahía Samborombón). We characterized the multivariate space occupied by the species, which was similar for the two assemblages. This characterization was more conspicuous when form variables (i.e., shape and size) were analyzed. Despite the tendency of sigmodontines towards omnivory, both assemblages had their species separated in the multivariate space by their dietary categories. The morphospace was structured by variables related to food intake and processing, including both shape and size of skulls and mandibles. Similar results were reported in a study in ctenomyid rodents (Morgan et al. 2017) that showed a morphospace structured mainly by craniodental and forelimb specializations related to fossoriality. A different tendency was observed by Álvarez et al. (2011) in caviomorph rodents, where ecological factors would not have great explanatory power over morphological variation. We did not assess size directly for the form variables PCAs, as all the morphological variables negatively correlated with the first component; hence size was assumed a latent variable and the loadings as evolutionary allometric coefficients (see Giannini et al. 2010; Flores and Casinos 2011; Cassini et al. 2015). Furthermore, removal of size (i.e., shape variables; Mosimann 1970) led to a higher, though not complete, overlapping in the morphospaces occupied by species of different diets (particularly in the extant assemblage). This provided supporting evidence to shape playing an important part in the observed segregation (as suggested by Jarman 1974; Bodmer 1989; Vizcaíno 2000; Vizcaíno et al. 2004, 2011). Graminivore species were the ones that stood out the most with the removal of size, as the most significant remaining variables after this procedure were associated with mandible robustness (e.g., SL, MRH, MAH). For example, we found long palate bridge opposed to condyle-incisive length, which can be associated with increased support for the teeth needed for chewing in this dietary group. Several authors (Vizcaíno and Bargo 1998; Bargo and Vizcaíno 2008; Álvarez et al. 2011; Cassini 2013) have suggested that mandibles reflect masticatory function better than skulls, which have undergone different selective pressures. This is consistent with observations documented for ungulates, where more robust mandibles with high mandibular rami and greater angular processes were associated with grazing feeding behavior (i.e., grass consumers) compared to browsing behavior (i.e., dicot feeders) (De Esteban-Trivigno 2011; Fraser and Theodor 2011a, b; Cassini 2013; Moyano et al. 2018).

Having accounted for the role of size, we used the multivariate space without its removal for the rest of the assessments. Different variables related to shape were highlighted by the analyses, and we could associate dietary tendencies to these variables. Mandible and skull robustness and large masseter muscle volume were associated with graminivore species, where masticatory muscles need more support than in the rest of the assemblage (similar results were reported by Maestri et al. 2016b). Broad palate and long snout were linked with larvivore species (consistently with Maestri et al. 2016b), where they would support an increased sense of smell and the use of the snout to root in the ground in search for prey (behavior documented for *Scapteromys aquaticus* by Massoia and Fornes 1964). Skulls with shorter palatal bridges, snouts and mandibles corresponded to insectivores and granivores, which could be associated with a short output lever arm of the masticatory lever system (see Cassini and Vizcaíno 2012 and references therein). However, this hypothesis remains to be tested. The multivariate analyses as a whole separated the species by body size and hardness of the preferred food item (PC1: smaller granivores on the most positive values and large graminivores on the most negative ones) as well as dietary preference of animals over plants (PC2: graminivores and granivores under negative values, and insectivores and larvivores under positive values, especially apparent on the analysis of the extant assemblage).

Regarding species' presence modifications, over the last 600 years, four species from the original assemblage were locally extinct (i.e., *Pseudoryzomys simplex, Necromys lasiurus, Necromys obscurus,* and *Bibimys torresi*), and one species (*Deltamys kempi*) was incorporated (Teta et al. 2013). The extinct species were one small graminivore and three large insectivores, and they covered the central area of the morphospace of the late Holocene assemblage, left empty in the extant one. Local extinctions significantly modified the overall shape of the assemblage morphospace as well as the amount of area covered, which was not compensated by the incorporation of a new species. Moreover, this study was performed using presence/absence to determine which species were part of the extant assemblage, but a more sensitive criterion would have implied greater morphospace changes. A change in the abundance of all the studied species has been documented on previous studies (e.g., Pardiñas 1999; Teta et al. 2013). Following what is expected for a disrupted environment, half of the remaining species abundances decreased significantly, while the four opportunistic species saw their abundances rise and are dominant in the extant assemblage. Particularly, the extant assemblage is dominated by the opportunistic *Akodon azarae, Oligoryzomys flavescens, Calomys laucha,* and *Calomys musculinus* (three granivores and one insectivore with a high preference for grains), with very low abundances of *Holochilus vulpinus, Reithrodon auritus* (graminivores), and *Oxymycterus rufus* (larvivore). If our study had considered a threshold in abundance, excluding these species from the extant assemblage, the morphospace covered would be lacking all the species under negative values of PC1 and PC2.

We associate the local extinctions and decreased abundance of sigmodontine rodents to anthropic effects in the area. Several authors have reviewed the impact of European settlements in the Humid Pampas (e.g., Montoya 1984; Soriano et al. 1991; Rapoport 1996; Zalba and Villamil 2002; Miñarro and Bilenca 2008; Tognetti et al. 2010; Azpiroz et al. 2012; Alberio and Comparatore 2014; Marrero et al. 2014; Molina et al. 2014); since the sixteenth century, it has been used for foraging of sheep and cows and, afterwards, for crops, among other industries. Such activities have resulted in severe landscape modifications, with introduction of foreign species and loss of environments and biodiversity. This is documented to have affected plant as well as arthropod species, thereby decreasing the food availability for most sigmodontines (Zalba and Villamil 2002; Miñarro and Bilenca 2008; Tognetti et al. 2010; Alberio and Comparatore 2014; Marrero et al. 2014; Molina et al. 2014). Crops may also imply an increased availability of seeds for granivores. Even though sigmodontines are generally omnivorous, we observed that dietary preference was related to a species extinction. As previously mentioned, three insectivores and one graminivore were locally extinct, while the four species reported to be most abundant in the extant assemblage have a preference for a granivore diet.

Native vegetation tends to respond negatively to invasive plant species, and this relationship has been documented in the Humid Pampas (e.g., Rapoport 1996; Zalba and Villamil 2002; Alberio and Comparatore 2014). Less cover, richness, and diversity of native plant species have been reported in farmlands as well as other anthropic environments. A graminivore whose fitness was related to the consumption of native plants would be expected to be affected as well. *Pseudoryzomys simplex*, the graminivore that was locally extinct, was the smallest of its group. This species is an open space grazer that, under the scenario of livestock farming, would have begun to compete with sheep and cows. It would have encountered a dramatic change in the abundance of the plants it originally fed on, especially when corn, wheat and soybean began replacing the original pastures. This species' regional extinction has also been linked with the decrease of humid grasslands resulting from drought and cattle's preference for these patches, according to eighteenth century reports (Montoya 1984; Teta et al. 2013). Even though it was among the most abundant sigmodontines of the late Holocene throughout the entire Humid Pampas, *P. simplex* is currently relegated to the northernmost latitudes of Argentina (Pardiñas et al. 2004). Competition with livestock and plant replacement would not have affected the remaining graminivores to this extent, although they implied a significant decrease in their abundance. *Reithrodon auritus*, another open space grazer, has a larger body size than *P. simplex.* Though it was not locally extinct, its abundance decreased significantly over the last centuries in the Humid Pampas (e.g., Pardiñas 1999). Regarding *Holochilus vulpinus*, it prefers grazing on riversides (Busch and Hodara 2010; Pardiñas et al. 2010a), which have been left unused for livestock farming and crops. These anthropic activities would not have been a severe problem for this species. Even though all three graminivores were affected by anthropic activities, only *P. simplex* was locally extinct. This could be related to its environmental preferences, or perhaps imply an adaptive disadvantage of being a small graminivore species.

The richness and diversity of plants and insects are intimately connected. Several studies have reported that land use intensification caused changes in abundance and richness of arthropod species, and that this is linked to richness of native plants (e.g., Marrero et al. 2014; Molina et al. 2014). In this scenario, the three largest insectivores (*Necromys obscurus, Necromys lasiurus,* and *Bibimys torresi*) were locally extinct from the Bahía Samborombón late Holocene assemblage. However, a new insectivore species (*Deltamys kempi*) appeared in the extant assemblage. There has been only one recent record for this species (Pardiñas and Teta 2015), so we cannot fully discard the possibility of it existing in the late Holocene in a low abundance that eluded our record. Nevertheless, the morphospace occupied by this species overlaps with that of the remaining insectivore (*Akodon azarae*). So it is not replacing any of the extinct species in their morphospaces, which may suggest an adaptive disadvantage of larger insectivores.

On the other hand, crops implied a switch from native seeds to implanted ones, but overall increased the stock of grains. Consistently, none of the three species of granivores were locally extinct, despite sharing overlapped regions of the multivariate space. Moreover, their abundances are reported to have increased (Teta et al. 2013). Thus, we interpret the effect of anthropic activity on granivores as favorable.

The taxonomic diversity and morphological disparity of the larvivores (*Scapteromys aquaticus* and *Oxymycterus rufus*) remained unchanged between both assemblages. At this point, no evidence of a negative or positive anthropic effect can be concluded for this dietary group. Despite the relative nutritional similarities between annelids, larvae, and hard shell arthropods, the pattern observed for insectivores is not extended to larvivores. Even though their size was similar to that of the locally extinct insectivores, the composition of larvivore species was unchanged between the two assemblages.

On a final note, as seen for other taxonomic groups, anthropic activities affected sigmodontine rodents, leading in some cases to local extinctions, and modifying the composition of the assemblage of Bahía Samborombón throughout the last 440 years. We would like to note that the morphospaces compared were calculated with the same specimens, so our analysis was not sensitive to temporal shape and size modification within the species. However, when comparing species of different genera, even if these modifications occurred, they would not have been large enough to modify the overall pattern. The recent local sigmodontine extinctions were not stochastically located on the multivariate space. The extinct species were either the largest of the insectivores or the smallest of the graminivores. Compared to the rest of the assemblage, these species were of intermediate size. However, larvivore species of similar sizes were not extinct, hence not being able to conclude that size was the only variable in effect. It remains to be tested if extinction of smaller graminivores and larger insectivores is a local phenomenon or a pattern with an underlying biological basis that can be extended to other assemblages. Our hypothesis is that there is a close link between size and energetic efficiency for different diets, which would imply that smaller graminivores and larger insectivores are more inefficient and therefore more vulnerable to extinction.

Different body sizes and morphophysiological adaptations have been associated with different dietary preferences (e.g., Perrin and Curtis 1980; Demment and Van Soest 1985; Ellis et al. 1995; Wang et al. 2003; Janis 2000, 2007; Clauss et al. 2008, 2009; Merritt 2010; Cassini 2013). Among mammals, there is a general pattern in which herbivores tend to large sizes and insectivores to small sizes. An evolutionary basis for this pattern may be attributed to the fashion in which two kinds of foods, insects or leaves, are metabolized. Insects have high protein content and are easily digestible, which ranks them as a highly valuable energy resource. Small animals have a higher basal metabolic rate per gram than larger animals (Peters 1983; Calder 1996; Brown and West 2000), thus insect consumption allows them to fulfill these energetic requirements. However, as we look at the total mass of the animals, larger ones have higher energetic requirements. As body size increases, the low abundance of insects then becomes an issue. Here is where herbivory appears as an alternative: plant availability is considerably higher than insect availability. As plant matter has lower protein content, larger quantities of food need to be ingested. Additionally, a graminivore diet is rich in cellulose, which is of slow digestion and requires symbiosis with microorganisms, as well as digestive tract adaptations to host them, and an increase of the time that food spends inside it. In non-ruminant animals, herbivory usually implies coprophagy: food needs to go through the digestive tract twice for the necessary nutrients to be absorbed. In summary, when plants are consumed, energy obtaining is slower, and this is associated with a lower metabolism than that of animals with a high protein diet (Grodziński and French 1983; Demment and Van Soest 1985; Wang et al. 2003). The simplified scenario for these two dietary alternatives is as follows: on one side, insectivory allows sustaining a high metabolism but is limited by the availability of insects, which becomes a problem for large size animals; on the other side, herbivory implies a slower digestion and lower metabolism, and requires digestive system adaptations that would not be viable in small sized animals with high energetic requirements. Even though this is not an absolute rule, and large sized insectivores exist (e.g., aardvark, anteaters), this tendency is represented in the assemblage studied in the present work: the largest sigmodontine species are herbivores, and insectivore species are among the smallest. If insectivory decreases its efficiency towards large sizes, then the largest insectivore species (in the Bahía Samborombón assemblage, *Necromys obscurus, Necromys lasiurus,* and *Bibimys torresi*) may have been relatively disadvantaged in respect to smaller ones. Likewise, the smallest herbivore species (in the Bahía Samborombón assemblage, *Pseudoryzomys simplex*) would have been relatively disadvantaged in comparison to larger ones. This would imply that the morphospace covered by the largest insectivores and the smallest herbivores would have been characterized by a disadvantage regarding energetic efficiency. In a scenario of dramatic changes affecting landscape and food availability, the species that occupied this portion of the morphospace would have been in a relative disadvantage compared to the rest, and we believe this may have led them to their extinction.

The present work contributes to understanding the anthropic effect on an assemblage of sigmodontine rodents of the southeast of Buenos Aires Province over the last 440 years. Our results expand the outlook originally presented by presence/absence and abundance variation studies. The ecomorphological approach made it possible to identify morphological traits and dietary preferences related to the extinction of some species, and pointed towards groups that might have been especially vulnerable.

Certain limitations of our work should be surpassed in future analyses. Phylogenetic information should be integrated to the skull measurements in order to estimate how much of the observed similarities are based on evolutionary history. Furthermore, expanding the range of our assessments by performing similar studies on other sites would allow us to know if our findings are restricted to the local assemblage of Bahía Samborombón or support the hypothesis of an underlying cause behind the pattern observed here.

Acknowledgements The authors wish to thank to Sergio Lucero (MACN-Ma), Sergio Bogan (FHNFA), Diego Verzi, and Itatí Olivares (MLP) for their excellent predisposition and access to mammal collections. Orientation provided by Julio Torres has been a great help in age determination of *Holochilus* specimens. We wish to acknowledge the assistance provided by Diego Peralta with the early version of the manuscript, by Karl Sandager, Juan Jelf, and Andrew Milton with English revisions, and by the reviewers. Our special thanks are extended to Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) and to Sociedad Argentina para el Estudio de los Mamíferos (SAREM) for the grants that partially funded the study of the collections, and to Sergio Vizcaíno for his guidance and support. This is a contribution to the projects PICT 201-0537, 2016-2665 Agencia Nacional de Promoción Científica y Tecnológica (ANPCyT), and CDD-CB 650-14 Universidad Nacional de Luján (UNLu).

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