

Potential Distribution of Fossil Xenarthrans in South America during the Late Pleistocene: co-Occurrence and Provincialism

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Abstract Species distribution models (SDMs) are helpful for understanding actual and potential biogeographical traits of organisms. These models have recently started to be applied in the study of fossil xenarthrans. SDMs were generated for 15 South American late Pleistocene xenarthrans: eight Cingulata (*Glyptodon clavipes*, *Doedicurus clavicaudatus*, *Panochthus tuberculatus*, *Neosclerocalyptus paskoensis*, *Pampatherium typum*, *Pampatherium humboldtii*, *Holmesina paulacoutoi*, and *Holmesina occidentalis*) and seven Folivora (*Glossotherium robustum*, *Lestodon armatus*, *Mylodon darwini*, *Catonyx cuvieri*, *Catonyx* (= *Scelidodon*) *chilensis*, *Megatherium americanum*, and *Eremotherium laurillardii*). Models were evaluated for three periods: the last interglacial (LIG), the last glacial maximum (LGM), and the Holocene climatic optimum (HCO). Co-occurrence records were studied based on the overlap of the potential distributions and compared with the available biome reconstructions of South America during the LGM to analyze species distribution patterns, ecological requirements, and possible interactions. Our results suggest the existence of provincialization within xenarthran megamammals grouped in at least three bioregions. Northern and southwestern taxa overlap in the Río de la Plata region where also some endemic taxa are found. We

observed overlapping potential distributions but separated and continuous realized distributions between closely related xenarthrans suggesting competitive exclusion. A generalized reduction in potential habitats at the end of the Pleistocene was not obvious as some taxa show stable potential areas during HCO when comparing with LGM. Nonetheless, fragmentation of the most suitable areas due to climate variation and the impact of reduction in available land due to sea level changes cannot be ruled out as involved in the extinction.

Keywords Folivora · Cingulata · Species distribution models · Paleobiogeography · Late Pleistocene · Last glacial maximum

Introduction

Species distribution models (SDMs) are helpful in understanding actual and potential biogeographical traits of organisms, and their use in paleobiogeography studies has recently increased (see Varela et al. 2011; Franklin et al. 2015). Compared to the classical narrative of biogeographic description of extant and fossil species, SDMs have the advantage of being capable to estimate past and future distributions and understand speciation and ecological processes, among others (Raxworthy et al. 2008; Blair et al. 2013; Torres et al. 2013; Gutiérrez et al. 2014). These models have been used to estimate variation in the distribution range of taxa in paleobiogeographical studies (Varela et al. 2011), but not to characterize areas in terms of the fossil taxa found in them.

Some studies have focused on SDMs of the South American Pleistocene megafauna (Lima-Ribeiro and Diniz-Filho 2012; Dantas et al. 2013; Gallo et al. 2013) and a few of them have dealt with xenarthrans, more specifically, with ground sloths (Lima-Ribeiro et al. 2012; Varela and Fariña

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2016). These latter studies showed a reduction in potentially suitable areas for ground sloth species at the end of the Pleistocene and also the overlap between the suitable areas of some taxa, particularly in the Río de la Plata region (Varela and Fariña 2016). Also, co-occurrence records of ground sloths in a single fauna are rare and it could be related to a heterogeneous landscape with a complex pattern of vegetation (McDonald et al. 2013; Varela and Fariña 2016).

There are several studies regarding paleobiogeographic aspects of fossil cingulates (Scillato-Yané et al. 2005; Carlini et al. 2008; Zurita et al. 2009a, b, 2011a, b; Zamorano et al. 2014), the other large clade of Pleistocene xenarthrans, but SDMs have not yet been applied to this group. Among them, glyptodonts are a particular group to study as, although there is evidence of differentiation in feeding habits between the taxa (Vizcaíno et al. 2011), all glyptodonts have been proposed to forage mostly near the ground based on their general body form. They must have been confined to a very narrow feeding zone regarding access to vegetation, and that would result in greater competition among glyptodonts than among other xenarthrans such as ground sloths (Vizcaíno et al. 2011). This could also have applied, to some extent, to the pampatheres (Vizcaíno et al. 1998, 2004; De Iuliis et al. 2000).

Therefore, the study of potential areas of distribution, as well as that of potential areas of co-occurrence of extinct species with equal or different ecological requirements, represents a valuable tool to infer paleoenvironmental conditions, interactions between species, and their evolutionary history. In this paper, we expand the Paleo-Species Distribution Models analyses in Varela and Fariña (2016) by including more ground sloths and introducing glyptodonts and pampatheres. Thus, we intend to evaluate ecological relations and to assess possible groupings of distinctive Pleistocene xenarthrans that correlate with biogeographical regions and provide information on their evolutionary history.

Material and Methods

Data of occurrences assigned to the last glacial maximum (LGM) at ~26.5 to 19.0 ka (Clark et al. 2009) were obtained from a review of the literature and from the Paleobiology Database (<http://paleobiodb.org>) for 15 South American late Pleistocene xenarthrans. The records included eight Cingulata (*Glyptodon clavipes*, *Doedicurus clavicaudatus*, *Panochthus tuberculatus*, *Neosclerocalyptus paskoensis*, *Pampatherium typum*, *Pampatherium humboldtii*, *Holmesina paulacoutoi*, and *Holmesina occidentalis*) and seven Folivora (*Glossotherium robustum*, *Lestodon armatus*, *Myiodon darwini*, *Catonyx cuvieri*, *Catonyx* (= *Scelidodon*) *chilensis*, *Megatherium americanum*, and *Eremotherium laurillardii*). The records of these taxa in South America used for our study are shown in detail in Table S1. We considered the

following taxa as monospecific for the late Pleistocene of South America: *Doedicurus* (Zurita et al. 2014), *Neosclerocalyptus* (Zurita et al. 2011b), *Glossotherium* (McAfee 2009), *Lestodon* (Czerwonogora and Fariña 2013), *Myiodon* (Esteban 1996), and *Eremotherium* (Cartelle et al. 2015). Regarding *Glyptodon*, we considered both *G. reticulatus* and *G. clavipes* records to be representative of the same species as has been suggested by Cuadrelli et al. (2015). In the case of *Panochthus* and *Megatherium*, only the most abundant species, *P. tuberculatus* and *M. americanum*, respectively, were considered for modelling, as other species lacked sufficient dated records. Finally, for *Catonyx*, we considered records of *C. cuvieri* and summed together records of the two other recognized species, *C. chilensis* and *C. tarijensis*, as they have been previously suggested to form a subgenus within *Catonyx* (McDonald 1987).

We obtained climate data from General Circulation Models (GCM) available at the WorldClim database (Hijmans et al. 2005; <http://www.worldclim.org/>) to reconstruct the paleoclimate for the last interglacial (LIG) at ~130 to 115 ka (Dahl-Jensen et al. 2013), the LGM, and the Holocene climatic optimum (HCO) at ~8 to 5.5 ka (Baker et al. 2001). Layers with spatial resolution of 30' for the LIG and 2.5' for the LGM and HCO were acquired. The data of LIG were upscaled by interpolation to the same resolution as the LGM and HCO for projection purposes (see Franklin et al. 2013). Climate data available at WorldClim is calibrated and statistically down-scaled from the PMIP2 LGM dataset (Braconnot et al. 2007; <http://pmip2.lsce.ipsl.fr/>). Seventeen bioclimatic variables available in the database were used in the analysis, which includes annual mean temperature, mean diurnal temperature range, isothermality, maximum temperature of warmest period, minimum temperature of coldest period, temperature annual range, mean temperature of wettest quarter, mean temperature of driest quarter, mean temperature of warmest quarter, mean temperature of coldest quarter, annual precipitation, precipitation of wettest period, precipitation of driest period, precipitation of wettest quarter, precipitation of driest quarter, precipitation of warmest quarter, and precipitation of coldest quarter.

The potential distribution of fossil xenarthrans was reconstructed by ecological niche modeling using the software MAXENT v.3.3.3 k (Phillips and Dudik 2008). MAXENT utilizes a maximum entropy approach to species distribution modeling with presence-only data (Phillips et al. 2006). Paleo-Species Distribution Models (PSDMs) were constructed for the LGM from occurrence records between 13 and 40 ka, assuming that the species were also present during the LGM. The obtained model was then projected to predict the species potential distribution during the HCO and LIG (according to GCMs).

As high correlation is expected between many variables, an initial run in MAXENT and a jackknife test were performed to

identify variables with minimal or no contribution to the models. Those variables were omitted and only a group of six significant variables were used in the final models. We ran each model 100 times with a random subsample of 25% of the occurrences dataset for model testing. Model performance was evaluated using the area under curve (AUC) statistic. An AUC value of 0.5 indicates a random prediction, whereas closer to 1 values indicate better predictive ability. A jackknife procedure was used to assess the contribution of the variables used in the modeling process. A qualitative evaluation was made by superimposing the records not used for model training onto the obtained maps.

Model results were further evaluated using the R package Phyloclim (Heibl and Calenge 2013). Niche Overlap between the species was evaluated using the statistics D and I (Warren et al. 2008) and Predicted Niche Occupancy (PNO) profiles (Evans et al. 2009) for the different species in relation to each environmental variable were created. To assess the existence of groups based on similar predicted niche we used D statistic to perform a cluster analysis with the software package Past (Hammer et al. 2001).

Data Availability Statement

All data generated or analyzed during this study are included in this published article [and its supplementary information files].

Results

Potential Distributions

Predicting capacity of the models was fairly high for most species with values of AUC over 0.8 (Table S2), although values for *Catonyx cuvieri* and *Pampatherium humboldtii* were close to 0.7 indicating less reliable models whose interpretation must be cautious.

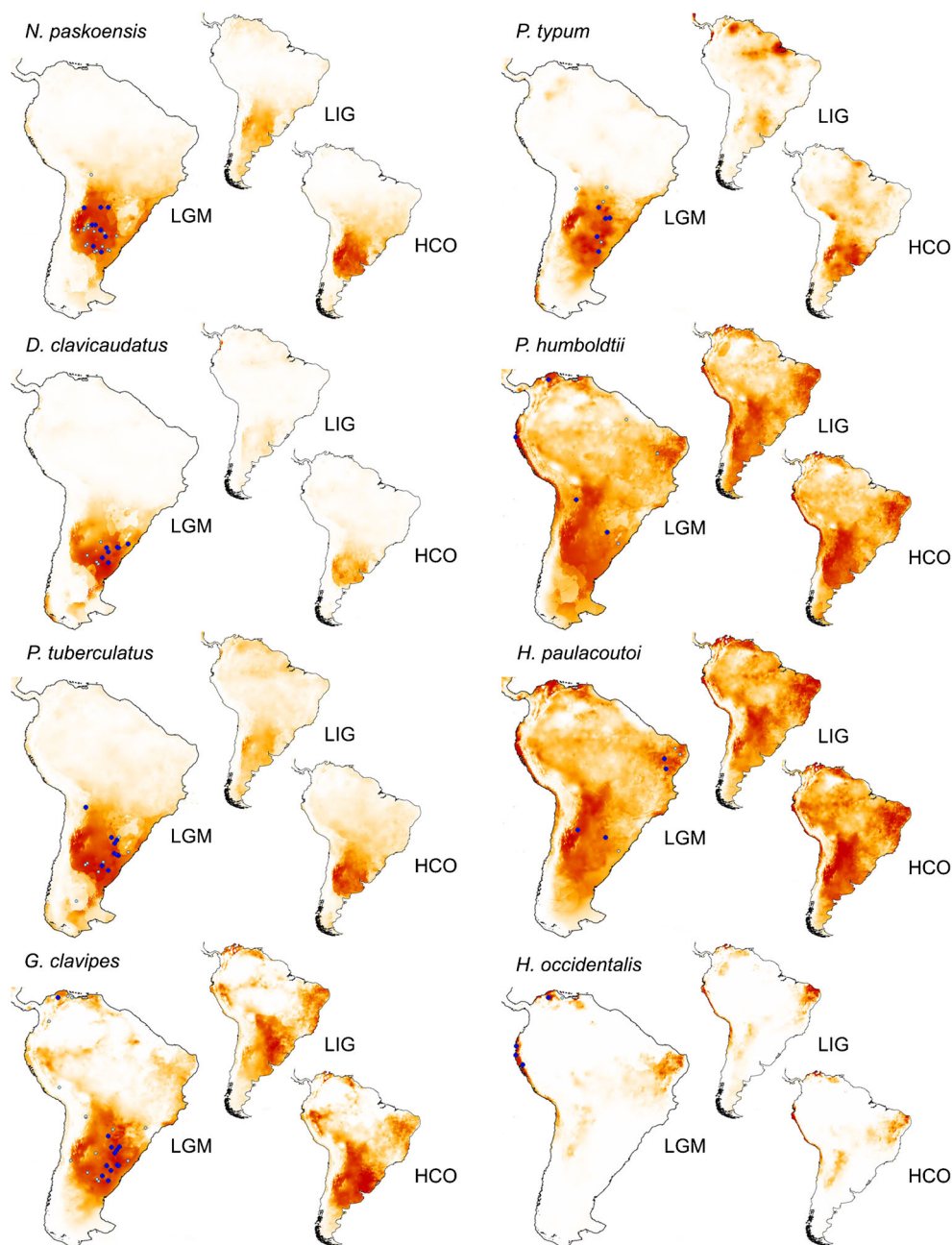
The predicted potential distribution during the LGM for glyptodonts (Fig. 1) showed a general pattern where most of the species displayed high probability of occurrence in the Chaco-Paraná Basin, the Pampas, and to some extent in Patagonia. *Panochthus tuberculatus* and *Glyptodon clavipes* exhibit the most southern areas with high probability of distribution, and the latter also presents high probability zones in the Pacific coast of Peru and Ecuador, the Caribbean coasts of Colombia and Venezuela, and the northeastern intertropical region of Brazil. In all species, the model projection for the LIG and the HCO showed a reduction in the suitable areas of the Chaco-Paraná Basin and the Pampas compared with the LGM, and in the case of *D. clavicaudatus* the projection for the LIG shows the most dramatic reduction of the distribution. On the other hand, for *Panochthus* and *Glyptodon*, more areas

of high probability appear in the northeastern intertropical region of Brazil during the LIG and the HCO.

For pampatheres (Fig. 1), two main trends can be observed. *Holmesina paulacoutoi* and *Pampatherium humboldtii* showed highly suitable areas during the LGM that expanded almost from Tierra del Fuego in the south to the Caribbean coasts in the north, with high probabilities in the Pacific and Atlantic coasts and the Amazon basin. On the other hand, *Holmesina occidentalis* and *Pampatherium typum* presented more restricted predicted areas. The potential distribution of *P. typum* is similar to that of glyptodonts, while the distribution of *H. occidentalis* is even more restricted only to small areas in the northeastern Brazil, the Caribbean coasts of Colombia and Venezuela, and the Pacific coast of Peru and Ecuador. Model projections on the LIG and HCO showed similar trends in *H. occidentalis*, *H. paulacoutoi*, and *P. humboldtii* with stable zones of potential distribution during the three periods and a slight increase in high probability areas in the HCO. On the other hand, the model for *P. typum* presented important changes in regard to its highly suitable areas. During the LIG, a reduction in potential areas is observed in the Chaco-Paraná Basin and the Pampas, but high probability zones are present in northern Brazil, the Guianas, and Venezuela, while HCO projection shows both high suitable areas in the Chaco-Paraná Basin and the Pampas and in northern zones in the Amazon basin.

The predicted distribution during the LGM for ground sloths (Fig. 2) showed that most species have areas of high probability in the southern cone, from the Chaco-Paraná Basin to Tierra del Fuego, and to some extent in the Andean region. Among them, *Glossotherium*, *C. cuvieri*, and *C. chilensis* also showed highly suitable areas in the Caribbean coasts and the northeastern intertropical region of Brazil. *Megatherium* showed predicted suitable zones in northern Andes in Peru, Ecuador, Colombia, and Venezuela, and *Lestodon* showed a more limited distribution, restricted principally to the Chaco-Paraná Basin and the Pampas. *Eremotherium* was the only studied sloth for which the potential distribution areas were almost exclusively in the northern regions of South America, including the Amazon basin, the intertropical region of Brazil, the Andean and the Pacific coasts of Peru and Ecuador, and the Caribbean coasts of Colombia and Venezuela. The model projection for the LIG and the HCO showed that only *L. armatus*, *M. darwinii*, and *C. chilensis* had substantial reduction in their suitable areas, and mainly during the LIG. In the other species, no major reduction in suitable areas can be observed. However, what appears more evident is the emergence of high potential areas in the southernmost regions compared to the LGM. This shift in the distribution is more notably observed in *Eremotherium*, for which the potential areas in the Amazon basin disappear during the LIG and the HCO.

Fig. 1 Potential distributions of cingulates for LGM and model projections for LIG and HCO. Larger dark points represent records used for training while smaller light points represent records not related to the LGM or lack of precise stratigraphic control



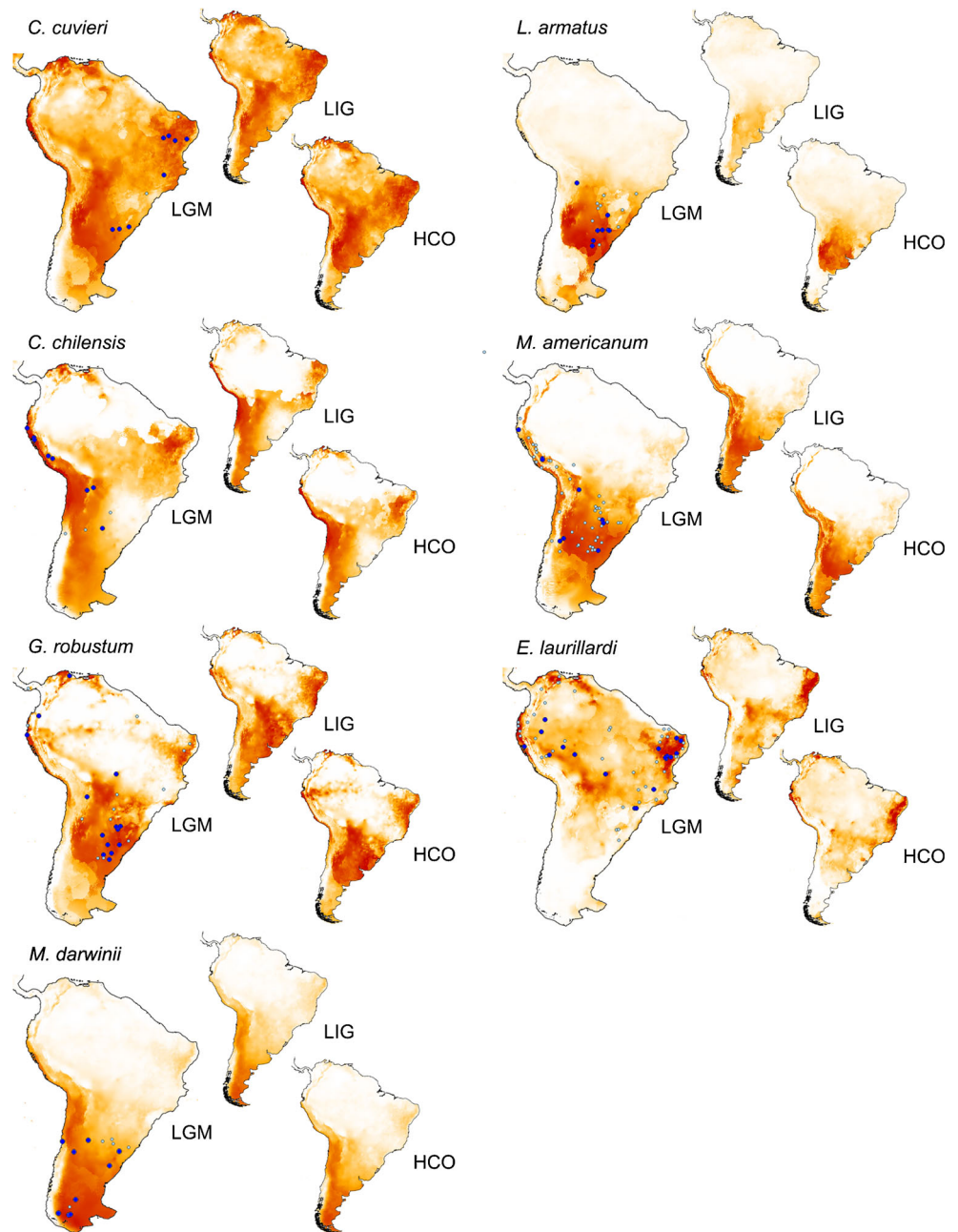
Predicted Niche Similarity

Table S3 shows the values of the statistics D and I indicating niche overlap between the studied species. The Cluster analysis based on the statistic D resulted in roughly three groups fairly supported by Bootstrap analysis (Fig. 3). The potential distribution areas of the group formed by *H. paulacoutoi*, *H. occidentalis*, *C. cuvieri*, *P. humboldtii*, *C. chilensis*, and *Eremotherium* (group 1) have a large latitudinal extent, and have an important presence in northern South America. A second group can be further divided in two. The potential distribution of both groups were mainly in the southern cone, but the group formed by *Lestodon*, *Neosclerocalyptus*,

Doedicurus, *Panochthus*, and *P. typum* (group 2) was more latitudinally restricted and concentrated in the Chaco-Pampean region, while the group formed by *Glossotherium*, *Glyptodon*, *Megatherium*, and *Mylodon* (group 3) has an important presence in the western coast and the Andean region.

Five climatic variables were the most relevant (Table S4): Isothermality (Iso), Mean Temperature of Wettest Quarter (MTWQ), Precipitation of Wettest Month (PWM), Precipitation of Coldest Quarter (PCQ) and, Temperature Annual Range (TAR); they feature in the majority of the species within the first six more contributing variables, and show good correlation with the cluster analysis groups. Accordingly, PNO profiles (Fig. 4) show that group 1 presents

Fig. 2 Potential distributions of folivorans for LGM and model projections for LIG and HCO. Larger dark points represent records used for training while smaller light points represent records not related to the LGM or lack of precise stratigraphic control



higher probability at lower PCQ, PWM, and TAR values; and higher MTWQ and Iso values. On the other hand, groups 2 and 3 present probability peaks at lower Iso and higher PCQ, but are further separated as group 2 shows lower MTWQ and higher TAR and PWM values; while group 3 presents lower PWM and nearly constant TAR values.

Discussion

In this paper, the expanded Paleo-Species Distribution Models analysis of fossil xenarthrans showed similar trends in glyptodonts, pampatheres, and ground sloths in highly

suitable areas predicted for the LIG, LGM and HCO, and suggest the existence of groups of Pleistocene xenarthrans that could be correlated to different bioregions.

During the LGM, the potential distributions of most cingulates and folivorans analyzed in this work have a large extension in the southern regions of South America, while a small group has potential distributions in northern regions. These observations are supported by the cluster analysis, in which two main groups are evident, largely in correlation with the most relevant climate variables. The lower values of Isothermality of the southernmost groups (groups 2 and 3) are characteristic of a climate with high variation of annual temperature in relation to day-night temperature oscillations,

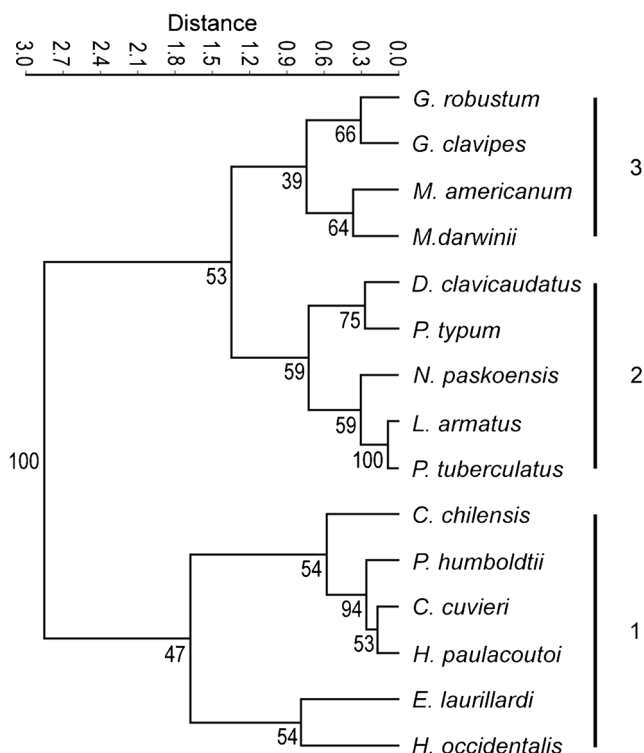


Fig. 3 Dendrogram showing cluster analysis results based on the niche similarity statistic *D*. Values indicate Bootstrap support. The three groups mentioned in the text are indicated

and could be correlated with Pleistocene biomes reconstructions (Ray and Adams 2001; de Vivo and Carmignotto 2004; Mayle 2006; Anhof et al. 2006; Fig. 5) representing temperate deserts and temperate grasslands. Furthermore, group 2's higher precipitation and lower temperature predicted requirements seem to limit their potential distribution, while group 3's flat probability distribution for temperature annual range and lower precipitation predicted requirements may indicate greater ecological tolerance and thus wider potential distributions. On the other hand, group 1's PNOs indicate both, annual and day-night, low temperature oscillations, and low precipitation, and could be related to tropical semi-desert or dry forest.

Thus, the groupings in the cluster analysis suggest the existence of provincialism between the studied xenarthrans with at least three bioregions related to different environmental conditions. Pleistocene mammal provincialisms have been noted before and related to pulses of expansion and contraction of steppes and tropical forests associated with glacial and interglacial periods (Ortiz-Jaureguizar and Cladera 2006). Generally, group 1's species showed a northern distribution and were linked to more tropical biomes, while group 3's species were related to colder environments and showed a southern distribution clearly associated with the Andean region. More interesting is the distribution of species in group 2, which concentrated in the Chaco-Paraná Basin and the area surrounding the Río de la Plata. Moreover, those areas also

represent the northeastern limit for group 3's species and the southern limit for group 1's species. Those regions could represent an ecotone between tropical and temperate ecosystems with the presence of a mixture of northern and southern taxa (Carlini et al. 2004; Oliveira and Pereira 2009; Gallo et al. 2013) and, more importantly, the presence of some endemic taxa like *Lestodon* and *Doedicurus* with more bounded distribution limits. Group 2 species' PNOs indicate adaptation to colder and humid environments that could be related to their distribution. Also, as noted by Varela and Fariña (2016), despite the prevalent dry conditions, the Río de la Plata region may have enjoyed a high productivity during the LGM due to the influence of the Paleo-Parana river and its possible floods (Fariña 1996, Sánchez-Saldías and Fariña 2014).

Potential co-Occurrence and Interactions

Overall, model results showed good predictive capacity and potential distributions in accordance with previous biogeographic works on Pleistocene megafauna (Cione et al. 2007; Varela and Fariña 2016). Nonetheless, two issues must be taken into account when discussing specific results. First, as mentioned above, low AUC values on *Catonyx cuvieri* and *Pampatherium humboldtii* make their predicted potential distribution less reliable. Second, the low number of training LGM records for some species, in particular pampatheres, may imply less accuracy in model predictions.

Co-occurrence is widely recorded between species within each group recovered in the cluster analysis and was clearly visible in the potential areas of distribution in our results. On the other hand, a more detailed view of potential distributions and recorded co-occurrences between species in different groups is interesting. In particular, cases of species with partial overlap in their potential distributions but not recorded co-occurring, which could be indicative of the existence of competitive exclusion (Gutiérrez et al. 2014).

As mentioned before, the potential areas of distribution of *Glyptodon* reach the northern and northeastern regions of South America, which is in accordance with some records in Colombia (Zurita et al. 2012) not used as training points due to lack of precise stratigraphic control. However, as recent studies have demonstrated (Oliveira et al. 2010; Zurita et al. 2012), *Glyptodon* is not present in northeastern South America and, incidentally, some authors have confirmed the presence of the North American genus *Glyptotherium* in Venezuela and northeast Brazil (Carlini et al. 2008; Oliveira et al. 2010). We did not analyze the potential distribution of *Glyptotherium* due to the lack of sufficient dated sites to include in the models, but the reported geographic distribution in northeastern South America overlaps with some potential areas reconstructed for *Glyptodon*. Moreover, this distribution agrees with the eastern corridor proposed as a dispersal route during the

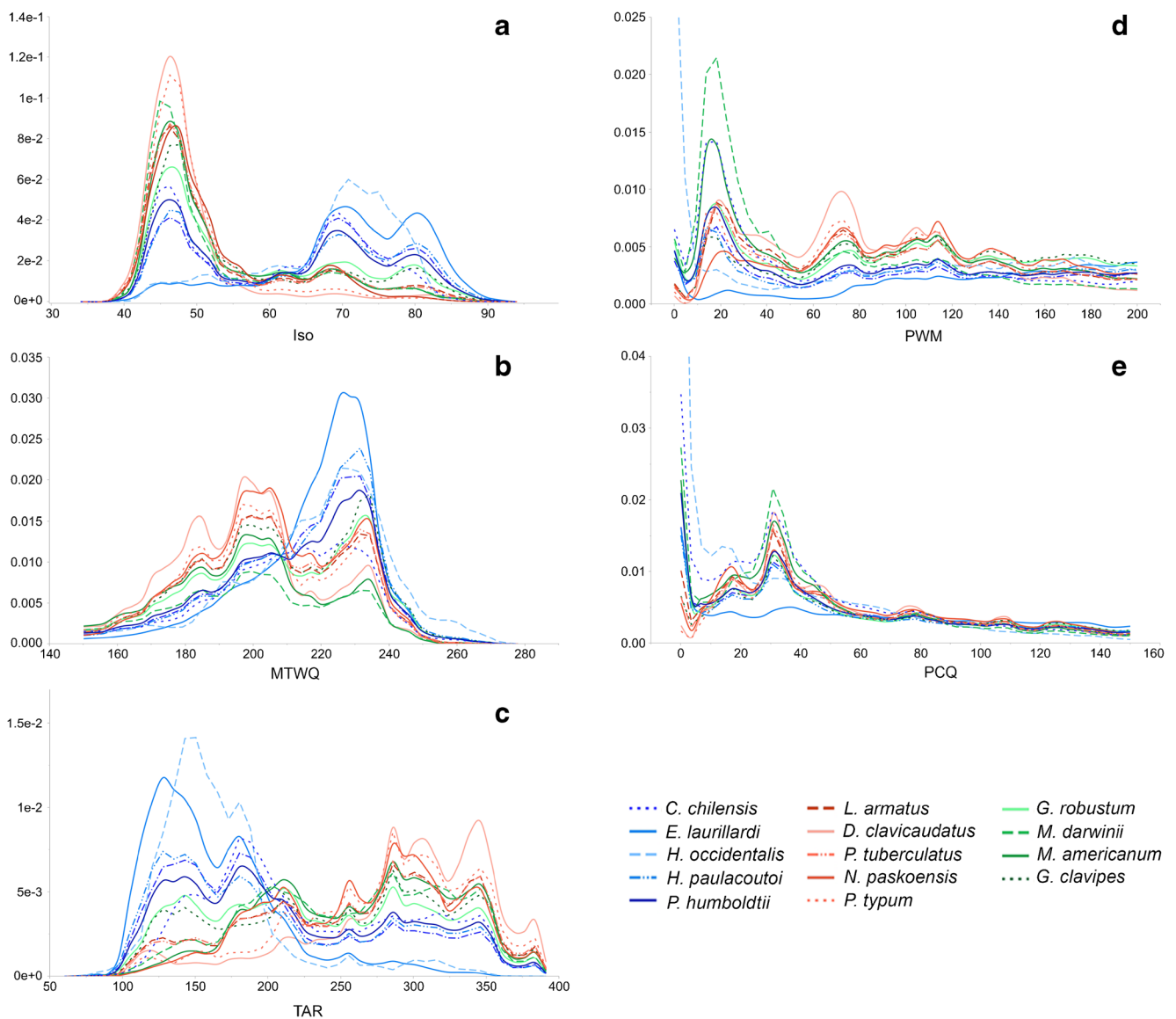


Fig. 4 Predicted niche occupancy profiles of the studied species for the five most contributing bioclimatic variables. **a** Isothermality (Iso). **b** Mean Temperature of Wettest Quarter (MTWQ). **c** Temperature Annual

Range (TAR). **d** Precipitation of Wettest Month (PWM). **e** Precipitation of Coldest Quarter (PCQ). Species are grouped according to cluster analysis results (see Fig. 3)

GABI for some clades (McDonald 2005; Zurita et al. 2012). Besides, there are no records of co-occurrence of *Glyptodon* and *Glyptotherium*. Therefore, the fact that some suitable areas for *Glyptodon* were occupied by *Glyptotherium* suggests the possibility that competitive exclusion might have occurred, given the unlikelihood of niche partitioning in such ecomorphologically similar taxa. Both genera have been considered grazers in open habitats (Fariña and Vizcaíno 2001; Pomi 2008), although, according to Vizcaíno et al. (2011), *Glyptodon* must have been a closed habitat selective feeder.

The remaining studied glyptodonts (*N. paskoensis*, *P. tuberculatus*, and *D. clavicaudatus*) present a more restricted distribution, with all of them included in group 2. Also, it is common to find some of these species co-occurring in the same locality, in particular with the inclusion of *Glyptodon*

(Tonni et al. 1985; Fariña et al. 2014; Kerber et al. 2014). It is worth noting that many records of *Panochthus* species in the Brazilian Intertropical Region were excluded as for most of these, the species lacks sufficient data, there is not a precise association with the LGM or a species-level identification is not available (Porpino et al. 2014). The co-occurrence of several species may imply some degree of niche partitioning among them. Vizcaíno et al. (2011) analyzed the hypsodonty index and relative muzzle-width and proposed that the large forms like *Panochthus* and *Doedicurus* could have been bulk-feeders in open environments, and the smallest forms like *Neosclerocalyptus* could have been bulk-feeders in relatively open environments. While the large *Glyptodon* appears more as selective feeder in closed habitats, an alternative possibility is that it had a different feeding behavior, browsing on specific

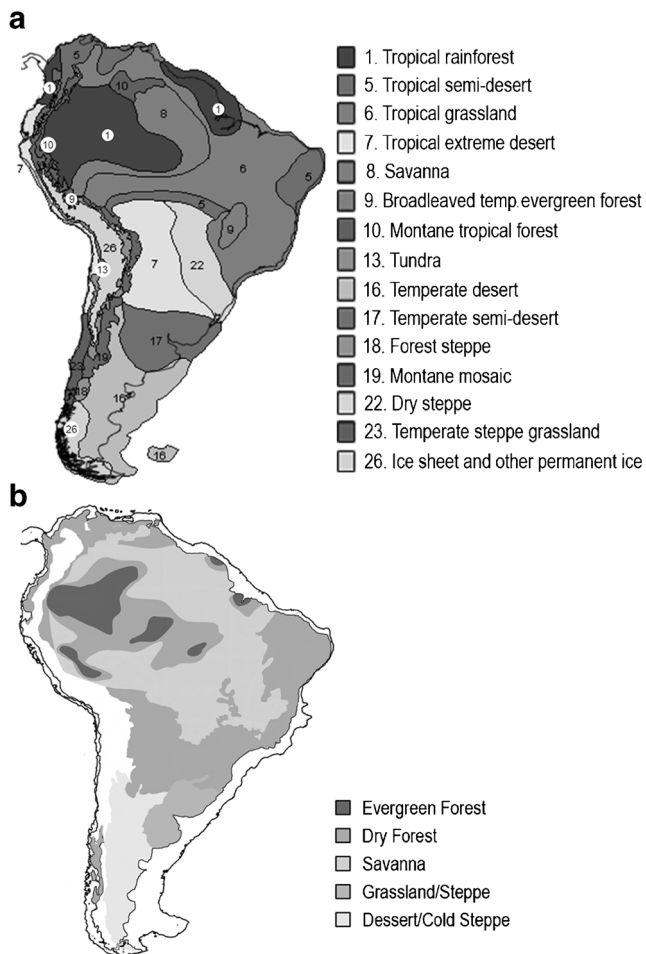


Fig. 5 LGM biomes reconstruction **a** modified from Ray and Adams (2001) and **b** based on de Vivo and Carmignotto (2004), Mayle (2006), and Anhuf et al. (2006) and modified from França et al. (2015)

plants or plant parts higher off the ground or that it may have had a more specialized physiology (Vizcaíno et al. 2011). According to the analysis of stable isotopes in *Glyptodon* by Domingo et al. (2012), it could have been a selective feeder in both open and closed habitats, which would indicate a flexible dietary behavior in this species.

For pampatheres, our results partially coincide with previous work on the paleogeography of the group (Scillato-Yané et al. 2005). The most important difference relates to *P. humboldtii*, whose occurrences used for training in our analysis are mainly on the west, contrary to the previously proposed distribution. Still, the potential distribution in our analysis overlaps with the results of Scillato-Yané et al. (2005). Moreover, the existence of some degree of overlap of potential areas between the taxa proves interesting, as their realized distributions are mainly parapatric.

De Iuliis et al. (2000) inferred all late Pleistocene pampatheres as grazers but suggested a differentiation on plant material hardness, indicating *Pampatherium* species as grazers of more abrasive vegetation than *Holmesina*. Also,

Scillato-Yané et al. (2005) proposed more extreme arid to semi-arid conditions for *Pampatherium* than *Holmesina* species. Considering our model's predictions and cluster analysis, only *P. typum* grouped differently, suggesting different environmental conditions that could relate to the temperate grasslands present in the Pampas. On the other hand, *P. humboldtii*, *H. paulacoutoi*, and *H. occidentalis* clustered together in group 1, indicating more tropical semi-arid environments. Nonetheless, taking into account the similarity between the species, the overlap of potential distributions and the lack of recorded co-occurrences on the same locality (although some species may be found together, Araújo-Júnior et al. 2013), some degree of competitive exclusion may be present between this pampather species and thus be responsible for the observed distributions.

In relation to *Megatherium* and *Eremotherium*, our results for the LGM show that these two genera have nearly no overlapping in their potential distributions. As expected, they cluster in different groups: group 3 and 1, respectively. This is consistent with the fact that no co-occurrences of the two are recorded (Nascimento 2008; Lima-Ribeiro et al. 2012), with exception of a single co-occurrence found by Oliveira et al. (2002) in the locality of Passo do Megatério, Rio Grande do Sul. However, that could have been the result of temporal averaging of alternating conditions due to the rapid changes in climate conditions during the late Pleistocene (Grootes et al. 2001; Scott et al. 2002; Scillato-Yané et al. 2005).

Model results show that *Megatherium* was adapted to temperate, arid, or semi-arid open habitats while *Eremotherium* was adapted to tropical to subtropical environments, which was also stated by Bargo and De Iuliis (1999), De Iuliis et al. (2000), and McDonald (2005). The lack of potential overlap between both genera correlates with the results obtained through the study of the masticatory apparatus of these sloths, with the high hypsodonty present in *Megatherium* (De Iuliis 1996) indicating an adaptation to arid to semiarid environments (Bargo 2001; Bargo et al. 2006a), in contrast with *Eremotherium* that showed lower hypsodonty (Bargo et al. 2006a) related to tropical to subtropical environments. Nonetheless, Bargo et al. (2006a) and Bargo and Vizcaíno (2008) suggested that differences in hypsodonty may be explained by a combination of variables, including diet, habitat, and behavior; for example, the hypsodonty index of *Eremotherium* is not quite different from the mylodontid sloths, whose potential distributions present in most cases strong differences with that predicted for *Eremotherium*, implying that other variables influenced those values.

Overall, the predicted potential distributions of *Megatherium* and *Eremotherium* support niche differentiation related to adaptation to different environments and probably not associated with resource partitioning or competitive exclusion.

On the other hand, potential distributions of *Lestodon* and *Megatherium* overlap in temperate arid to semi-arid regions, with various sites where the two genera co-occur (Tonni et al. 1985; Ubilla and Alberdi 1990; Coltorti et al. 2007; Martínez and Gutiérrez 2011), possibly indicating lack of competition and therefore niche differentiation. Accordingly, Bargo et al. (2006b), through the analysis of the muzzle in sloths, interpret *Lestodon* as a bulk-feeder (i.e., mainly grazer) and *Megatherium* as a selective feeder. Our results are in accordance with those of Bargo et al. (2006b) supporting some degree of resource partitioning between these sloths.

Regarding *Catonyx*, while both studied species clustered in group 1, *C. cuvieri* showed a wider potential distribution covering most of the continent. *Catonyx chilensis* showed highly suitable areas in the Brazilian intertropical region overlapping with zones where *C. cuvieri* is recorded, and reciprocally, the latter showed high probability areas in Andean regions where *C. chilensis* is recorded. The existence of overlap in potential distributions but the lack of recorded co-occurrence as well as a clear geographical difference in occurrence records suggest some degree of competitive exclusion between both species. Previous suggestions about habitat preferences of these taxa relate *C. cuvieri* to tropical rainforest and *C. chilensis* to dry forests (McDonald 1987), while Casamiquela (1970) and Zurita et al. (2004) suggested semi-desert and arid conditions to *C. chilensis* areas of distribution. Comparing our results with the proposed South American Pleistocene biomes reconstructions, a preference for arid open environments is clear for both species. However, considerably ecological tolerance is evident, in particular for *C. cuvieri*, which could be related to more forested habitats.

Concerning model projections, there are no common patterns between the studied species as some have clearly reduced high suitability areas during the LIG and HCO, while others, like *G. clavipes*, *H. paulacoutoi*, *P. humboldtii*, and *C. cuvieri* seem to be largely unaffected. So, making any statements about the potential role of climate change on the extinction probability of those species at the end of the Pleistocene is daunting. In any case, the cyclic pattern of expansion and reduction of steppes and tropical forests in South America during the Quaternary (Ortiz-Jaureguizar and Cladera 2006) may have produced fragmentation of highly suitable open-arid environments for most of the large xenarthrans during interglacial periods. This pattern can be seen in many species in our results, in which high probability areas tend to be more limited and lower probability areas connecting them are less prominent during the interglacials. Also, it is worth mentioning that as noted by Varela and Fariña (2016) almost in all cases the studied species showed high probability of presence in lands now submerged but exposed during the LGM, clearly contributing to the fragmentation of the potential distributions during the interglacials.

Final Remarks

Species Distribution Models have the advantage over narrative biogeography of being capable to estimate past and future distributions and understand speciation and ecological processes.

We expanded previously PSDMs analysis of fossil xenarthrans, and showed the existence of similar trends in glyptodonts, pampatheres, and ground sloths of highly suitable areas predicted for the LIG, LGM, and HCO. The presence of regions inhabited by phylogenetically distant xenarthrans suggests the existence of provincialism mainly associated with different environments. Also, our results support the existence of an ecotone in the Río de la Plata region with a mixture of northern and southern taxa and, more notably, the presence of some endemic species. This could be indicative of stability of the ecotone during the Pleistocene with consequences on diversification of taxa.

On the other hand, we observed overlapping potential distributions but separated and continuous realized distributions between closely related xenarthrans, which summed to the lack of co-occurrence records suggesting competitive exclusion as the main factor acting over their distributions.

Finally, a generalized reduction in potential habitats at the end of the Pleistocene was not obvious as some taxa show stable potential areas for the HCO when comparing with LGM results. Nonetheless, fragmentation of the most suitable areas due to climate variation and the impact of reduction in available land due to sea level changes cannot be ruled out.

This approach yields robust results that can be improved in two ways, as more taxa and chronologically precise records are added and also as the models utilized are refined. New studies should further focus on possible Pleistocene xenarthrans biozones and their relations to current patterns of provincialism in South America.

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