Research Article

Species distribution modeling reveals the ecological niche of extinct megafauna from South America

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Abstract

Climatic and environmental changes, as well as human action, have been cited as potential causes for the extinction of megafauna in South America at the end of the Pleistocene. Among megamammals lineages with Holarctic origin, only horses and proboscideans went extinct in South America during this period. This study aims to understand how the spatial extent of habitats suitable for *Equus neogeus* and *Notiomastodon platensis* changed between the last glacial maximum (LGM) and the middle Holocene in order to determine the impact that climatic and environmental changes had on these taxa. We used species distribution modeling to estimate their potential extent on the continent and found that both species occupied arid and semiarid open lands during the LGM, mainly in the Pampean region of Argentina, southern and northeastern Brazil, and parts of the Andes. However, when climate conditions changed from dry and cold during the LGM to humid and warm during the middle Holocene, the areas suitable for these taxa were reduced dramatically. These results support the hypothesis that climatic changes were a driving cause of extinction of these megamammals in South America, although we cannot rule out the impact of human actions or other potential causes for their extinction.

Keywords: Climatic changes, *Equus*, *Notiomastodon*, Quaternary, Paleoecology, Extinction

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INTRODUCTION

Equidae and Proboscidea are the only lineages of South American megamammals with Holarctic origins that went extinct at the Pleistocene/Holocene transition (Avilla and Mothé, 2013; Machado et al., 2018). The South American diversity of equids and proboscideans was low, mainly represented by *Equus neogeus* (Lund, 1840) and *Notiomastodon platensis* (Ameghino, 1888), respectively (Mothé et al., 2017a; Machado and Avilla, 2019). Both species were highly polymorphic, suggesting great genetic variability within the lineages. In addition, *E. neogeus* and *N. platensis* were widely distributed across the South American continent, with records from the high altitudes of the Andean Cordillera to the coastal and inland plains (Mothé et al., 2012, 2017a; Machado et al., 2018; Machado and Avilla, 2019).

The Proboscidea's arrival to South America is possibly related to the first migratory pulse of the Great American Biotic Interchange (GABI 1), just after the uplift of the Panamanian Isthmus ca. 3.1–2.8 million years ago (Woodburne, 2010). Although Proboscidea may have arrived earlier (Campbell et al., 2000), they are one of the most common megamammals in Quaternary sites, especially those that date to the middle to late Pleistocene (Mothé et al., 2012, 2017a). Paleoecological inferences suggest that *N. platensis* had an opportunistic/generalist feeding habit, consuming grasses, branches, leaves, and fruits (Mothé et al., 2017b; González-Guarda et al., 2018), which may have influenced its wide geographic distribution in South America.

After an extensive review of South American fossil horses, Machado et al. (2018) and Machado and Avilla (2019) considered *E. neogeus* as the only valid species for *Equus* in this continent (Barrón-Ortiz et al., 2019), reinforcing the importance of updated taxonomy for paleoecological and biogeographic studies (de Oliveira et al., 2020). The origin of *Equus* possibly occurred during the early Pleistocene of North America, with subsequent dispersion to South America during GABI 3 and GABI 4 (between 0.8 Ma and 0.125 Ma; Woodburne, 2010; MacFadden, 2013; Rook et al., 2019). Based on cranial and dental morphology, the Pleistocene *Equus* is considered a restricted grazer, and thus an indicator of open and arid environments (MacFadden, 2005; Semprebon et al., 2016). Furthermore, stable isotopes of equids from different localities from the Pleistocene of South America revealed distinct carbon and hydrogen values for *E. neogeus*, indicating variations in C_3 vegetation (possibly grass), C_4 grass, and a mix of C_3 and C_4 vegetation (Sánchez et al., 2004).

The combination of these paleoecological features suggests that *N. platensis* and *E. neogeus* should have been less vulnerable to negative pressures of natural selection during the Pleistocene/Holocene transition. Indeed, Mann et al. (2019) proposed that several characteristics of the megafauna (e.g., low reproductive

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rates, large size, and body mass) could have been advantageous for their survival under the unstable environmental and climatic conditions that prevailed after the last glacial maximum.

Species distribution models (SDMs) have become a popular tool to determine the potential geographic distribution of now-extinct species (Nogués-Bravo, 2009) and Quaternary megafaunal extinction dynamics (Lima-Ribeiro and Diniz-Filho, 2012). In general, species distribution models require occurrence records of the species under study, as well as bioclimatic variables, and employ analytical models to relate species occurrences to bioclimatic predictors. However, SDMs vary from the Hutchinsonian niche concept in that they are based only on abiotic data and occurrence records, and disregard dispersal and inter- and intraspecific interactions. Nonetheless, the result—a potential geographic distribution (PGD) map—can identify areas with environmental conditions similar to the localities of known species occurrences and show the variation in habitat suitability for species survival across the landscape (Guisan et al., 2002; Soberón and Peterson, 2005; Franklin, 2009; Lima-Ribeiro and Diniz-Filho, 2013).

Thus, considering the great resilience of *N. platensis* and *E. neogeus*, and the hypothesis that climate changes affected their population dynamics and geographic distribution during the LGM, we applied an SDM to help to understand their ecological niches and to recognize the influence of changing climatic conditions in South America on their extinction during the late Quaternary. We note, however, that the climate change hypothesis does not exclude a possible overkill scenario nor a combination of climate change and human action as the driver of the megafauna extinctions (Cione et al., 2003; Koch and Barnosky, 2006; Sandom et al., 2014).

METHODS

We used an SDM to determine the potential geographic distribution for *N. platensis* and *E. neogeus* during the LGM (Ray and Adams, 2001) and to estimate their suitable areas (SA) during the middle Holocene (6 ka; Melo and Marengo, 2008). First, the geographic distributions of *N. platensis* and *E. neogeus* were reviewed, considering only specimens identified at the species level by the most recent and reliable taxonomic reviews (Mothé et al., 2017a; Machado and Avilla 2019). We obtained georeferenced information for the fossil occurrences from previous studies that were referenced to the World Geodetic System 1984 (WGS 84) (Supplemental Table 1). Occurrence records were georeferenced to the WGS 84 and the Geographic Coordinate System in decimal degrees. Our database comprises records dated between 25–15 ka (LGM interval; Ray and Adams, 2001); records outside this temporal interval were not included.

We combined the selected occurrence records with bioclimatic data to project the potential geographic distribution of the two species during the LGM and middle Holocene (Franklin, 2009; Nogués-Bravo, 2009). The predictive maps were generated in Maxent v.3.3.3k (Phillips et al., 2006), which is based on an algorithm that estimates the species' distribution through maximum entropy modeling to predict the SA according to the potential niche of the species (Coelho et al., 2016). The Maxent program uses only occurrence data and background points of the species (Anderson et al., 2003) because absence data are often rare and unreliable, especially for extinct species (Amaro and Morais, 2014).

Ten thousand background points were sampled and 25% of the original occurrence dataset points were randomly selected to test the predictions and to evaluate the performance of the models

(see Barve et al., 2011; Owens et al., 2013). Additionally, five replicates of the models were used to generate the final model. Runs were conducted with a logistic output format, resulting in a map of habitat suitability of the species ranging from 0 to 1 per grid cell. The parameterization was adjusted according to specific characteristics of the species and the data used in the modeling following the recommendations of Merow et al. (2013). The models were evaluated by producing the receiver operating characteristic curve and calculating the area under the curve using the maximum training sensitivity plus specificity as the threshold value (Basher et al., 2014). Cross-validation was performed to evaluate the model accuracy.

We extracted layers of bioclimatic variables from the WorldClim Project version 1.4 (Hijmans et al., 2005) for 21 ka (LGM) and 6 ka (middle Holocene), which provides 19 variables from several general circulation models. In this study, the LGM layers were used as the model predictors and the middle Holocene layers as the model projections. The bioclimatic variables were downloaded at a spatial resolution of 2.5 arc-minutes, and the general circulation model used was the Model for Interdisciplinary Research on Climate-Earth System Model (MIROC-ESM; Watanabe, 2011). Only temperature and precipitation variables were included, resulting in a high correlation between the bioclimatic layers. Because it is recommended against using layers with highly correlated variables, the multicollinearity of climatic data was examined using the Pearson correlation coefficient, and the least correlated layers were then selected (Guisan and Thuiller, 2005; Giannini et al., 2012). The variables used for *E. neogeus* were mean diurnal range, mean temperature of warmest quarter, annual precipitation, and precipitation seasonality. For *N. platensis*, the variables used were diurnal range mean temperature of warmest quarter, precipitation of wettest month, and precipitation of warmest quarter. We estimated the continental surface area of South America in each generated map using ImageJ software (Abràmoff et al., 2004), considering sea level variations from the LGM to the middle Holocene and their influence on the South American continental-plain surface area (Stevaux, 2000). In addition, the suitable areas (SA) on each map were estimated with the Analyze Particles tool at a spatial scale of 1000 km. This method helps understand the changes in maximum suitability areas during the LGM and middle Holocene because it considers the differences in surface area of the continental region of South America in the LGM and middle Holocene due to eustatic movement.

RESULTS

The review of distribution data identified 198 localities for *E. neogeus* and 142 for *N. platensis*, all within the LGM interval. *Equus neogeus* was recorded from northern Venezuela, Colombia, Ecuador, Peru, Bolivia, Chile, Brazil, Uruguay, and the Pampean region of Argentina, whereas *N. platensis* was recorded across all South American countries except for Guiana, French Guiana, and Suriname (Fig. 1). The co-occurrence of the two species during the late Pleistocene in some localities resulted in similar patterns of geographic distribution, including some overlapping areas (Fig. 1). No SA were predicted below 42°S during the LGM, lower than the Huincul Fault zone (Figs. 2, 3). Data provided by Maxent indicate that predictor variables, average precipitation, and precipitation of wettest quarter increasingly contributed to the probability of occurrence of *E. neogeus* and *N. platensis* (see Supplemental Data).

During the LGM, the potential geographic distribution for *E. neogeus* and *N. platensis* (Figs. 2, 3) predicted that most of
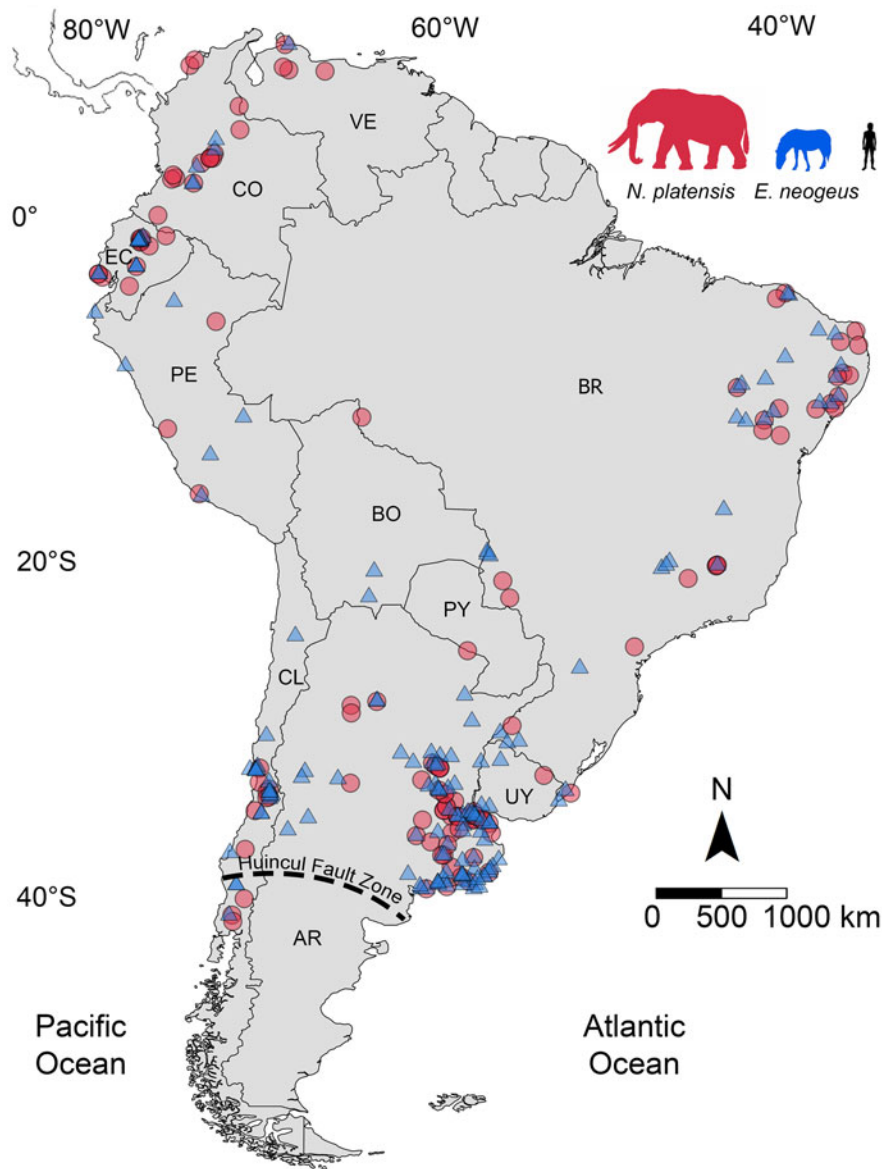
Figure 1. Geographic distribution of *Equus neogeus* (blue triangle) and *Notiomastodon platensis* (red circle) during the last glacial maximum (25–15 ka) in South America. Note almost complete superimposition of the geographic distribution areas of both species and their absence in the northern central region of the continent. Abbreviations: VE = Venezuela; CO = Colombia; EC = Ecuador; PE = Peru; BR = Brazil; BO = Bolivia; PY = Paraguay; CL = Chile; UY = Uruguay; AR = Argentina. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.). The approximate height for a human is 1.8 meters. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

the SA were in the Pampean region, southern and northeastern Brazil, Uruguay, southern Bolivia, northern Paraguay, northern and south-central Chile, Ecuador, Colombia, and Venezuela. The estimated potential distributions also showed suitability for both species in the Pampean region, southern and northeastern Brazil, and some small warmer areas (highly SA) throughout the Andes. However, during the middle Holocene, SA remained in the same regions where they were in the LGM, but contracted, with a southern shift in suitable habitats post-LGM.

DISCUSSION

The ecological niches of *E. neogeus* and *N. platensis* are inferred from palynological and paleodietary data, SDMs (such as this study), and comparisons with climatic models. The two species studied here are open and dry environment dwellers based on the superimposition of the patterns of each SA and the South American biomes reconstructions for the LGM (Ray and Adams, 2001; Behling, 2002; Cook and Vizy, 2006). During the LGM, *E. neogeus* often occurred in open and arid areas that were dominated by tropical and temperate semi-desert biomes (Ray and Adams, 2001; Behling, 2002; Cook and Vizy, 2006). Sánchez et al. (2006) suggested that late Pleistocene *Equus* populations might have restricted their use of habitats due to their exclusively grazing diet, which is a more selective feeding habit. Modeling of the potential distribution of *N. platensis* during the LGM suggested that this species occurred in areas with lower temperature and high aridity, such as tropical and temperate semi-deserts.

The Pampean region of Argentina during the LGM was predominantly a temperate semi-desert with a small area of temperate
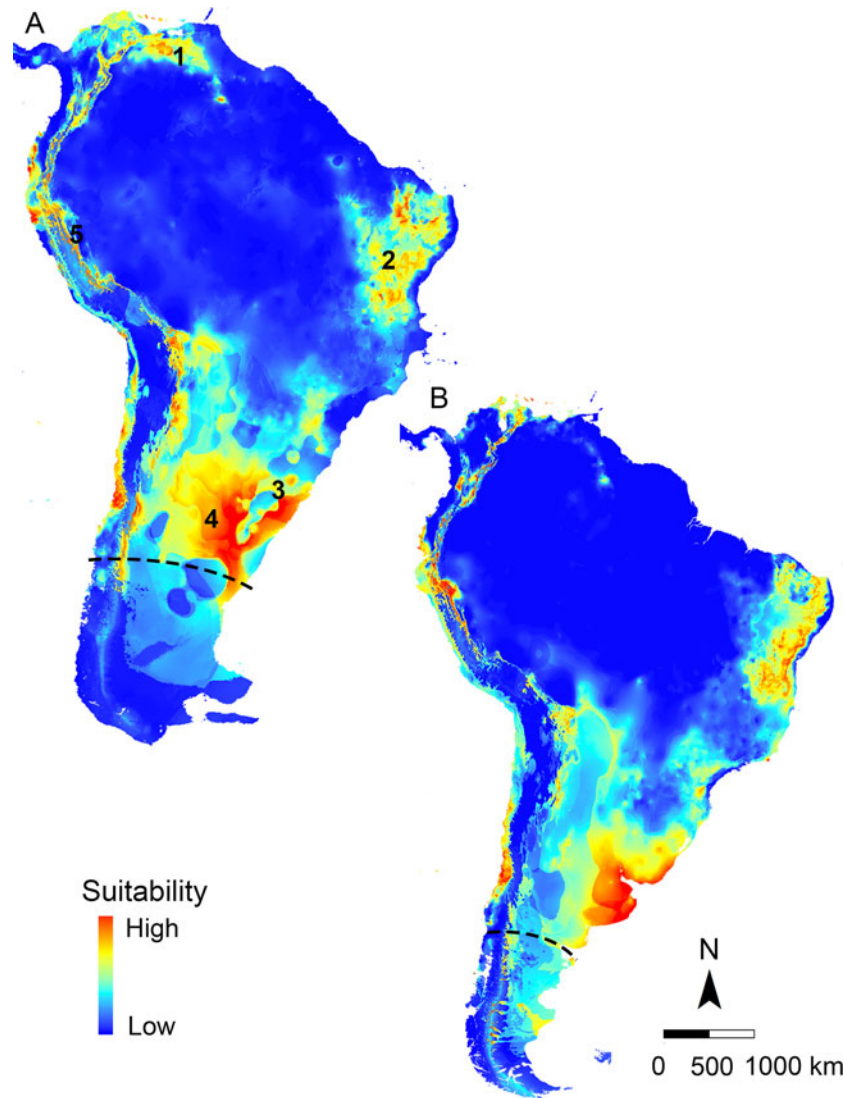
Figure 2. (color online) Potential geographic distribution of *Equus neogeus during (A) the last glacial maximum (25–15 ka), and (B) middle Holocene (6 ka)* of South America. Note that when comparing the LGM and middle Holocene patterns of potential geographic distributions, the potential distribution areas for *E. neogeus* show an enlargement during the LGM (A) in: (1) northern South America, (2) northeastern Brazil, (3) southern Brazil and Uruguay, (4) the Pampean region of Argentina, (5) and some small, warmer areas throughout the Andes. Dashed line represents the Huincal Fault Zone.

desert, characterized by low and dense vegetation, dry climate, low precipitation, and large daily temperature fluctuations (Iriondo and Garcia, 1993; Ray and Adams, 2001). During the LGM, southern Brazil had a drier and cooler climate than today. It was a period marked by the contraction of tropical and araucaria forests and the great expansion of grasslands (Behling, 2002), and, as Ray and Adams (2001) demonstrated, tropical semi-desert and tropical grasslands were the dominant landscapes in northeastern Brazil. The tropical semi-desert Caatinga biome is an open landscape with 2–10% vegetation cover of scattered grasses and small shrubs. Tropical grasslands are characterized by >20% vegetation cover, mainly grasses, with <5% woody plants (Ray and Adams, 2001). Based on the palynological record, Mayle et al. (2008) classified the vegetation cover of the region as a mix of Caatinga, xerophytic plants, and grass field. The xerophytic vegetation described in palynological studies suggests the predominance of an arid climate during the LGM. During the Pleistocene/Holocene transition in northern Chile, González-Guarda et al. (2018) suggested the

predominance of a woodland-mesic environment C_3 grassland with a significant presence of trees. For the south-central Chile region, González-Guarda et al. (2018) suggested a temperate environment, with a cold and humid climate, dominated by C_3 plants and with a significant woodland cover.

The middle Holocene projection revealed a noticeable reduction in SA for both species, approximately 19% and 16% for *E. neogeus* and *N. platensis*, respectively. The fact that *E. neogeus* was more commonly found in wide-open habitats than *N. platensis* might explain the larger reduction in its SA because those were the areas more affected by climate change. Additionally, although *N. platensis* is more frequently found in open areas, it also occurred in dense forests (Campbell et al., 2000; Codrea and Diaconu, 2007; Mothé et al., 2017a). Thus, *N. platensis* might have occupied both habitats. Despite the clear reduction in the potential SA for both species, there was a slight increase in the SA in the southernmost part of South America during the middle Holocene. This change might be related to the climatic/environmental variations that
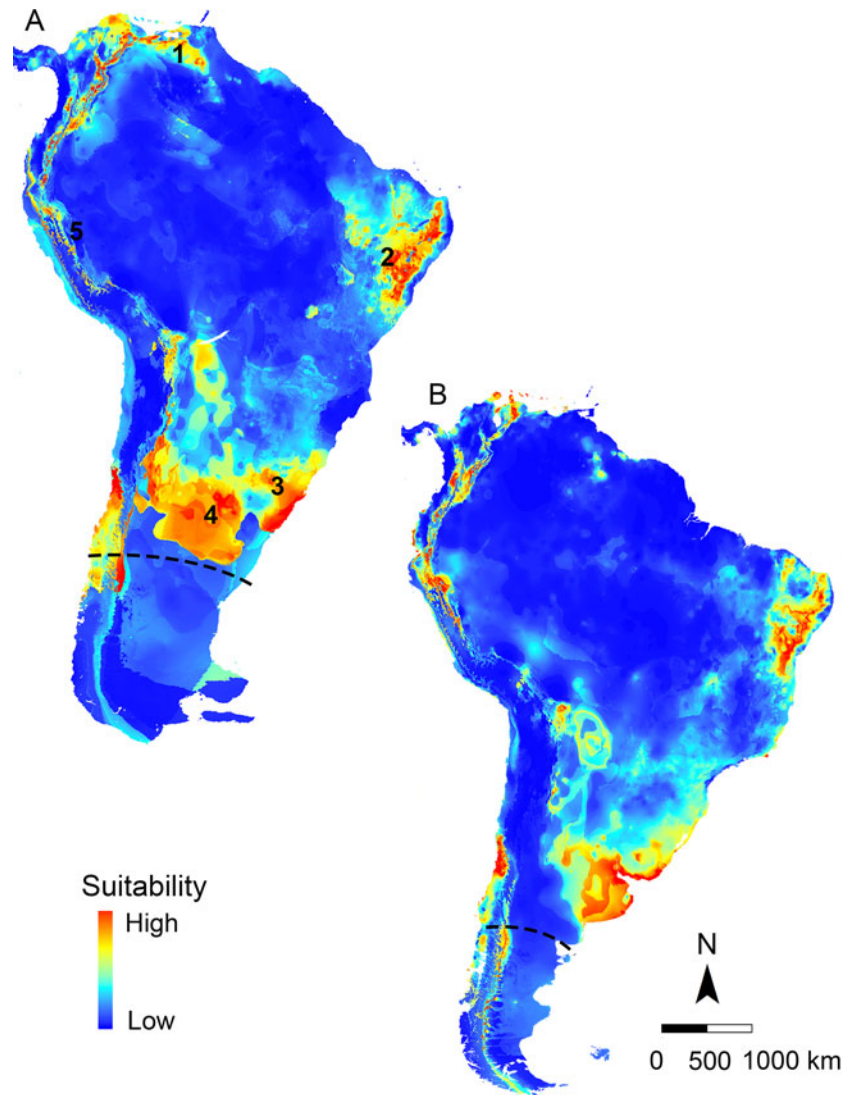
Figure 3. (color online) Potential geographic distribution of *Notiomastodon platensis* during (A) the last glacial maximum (25–15 ka) and (B) middle Holocene (6 ka). Note that when comparing the LGM and middle Holocene patterns of potential geographic distributions, the potential distribution areas for *Notiomastodon platensis* show an enlargement during the LGM (A) in: (1) northern South America, (2) northeastern Brazil, (3) southern Brazil and Uruguay, (4) the Pampean region of Argentina, (5) and some small, warmer areas throughout the Andes. Dashed line represents the Huincal Fault Zone.

occurred at the Pleistocene/Holocene transition, when both species likely searched for colder environments.

The middle Holocene projections showed that the SA were associated with a climate that was more humid than in the LGM (and slightly drier than today), except for northeastern Brazil, where humidity was estimated to be 10% higher during the LGM (Valdes, 2000; Melo and Marengo, 2008; Silva Dias et al., 2009; Prado et al., 2013). Palynological data suggested that the Argentine Pampean region climate was more humid during the middle Holocene (Prieto, 1996). In southern Brazil, the climatic model generated by Silva Dias et al. (2009) indicated the middle Holocene climate was slightly more humid with vegetation cover of mixed humid forest/tropical forest. In their climate models, Melo and Marengo (2008) suggested the occurrence of a warming signal during almost the entire year. According to Behling (1995), the palynological record indicated a reduced forest cover, suggestive of a drier climate. In northeastern Brazil, palynological data indicated that gallery forests were more developed during the middle Holocene (de Oliveira, 1999), which also

suggests a wetter climate (Melo and Marengo, 2008; Silva Dias et al., 2009; Prado et al., 2013). The vegetation models by Silva Dias et al. (2009) indicated that the vegetation of northeastern Brazil was characterized mainly by dry tropical forests/savannas, and a small area covered by seasonal tropical forests.

According to the fossil record and our SDM/PGD (species distribution/potential geographic distribution) models, *E. neogeus* and *N. platensis* had large areas of suitable habitat in arid environments with open vegetation during the LGM (Roig-Juñent et al., 2006). In both models, these species did not predominantly occupy dense forest environments such as the Amazon. Also, the SA for *E. neogeus* and *N. platensis* were more continuous and showed maximum suitability in the regions surrounding the La Plata River, the Pampean region in Argentina, and southern Brazil (Ramos et al., 2004). Moreover, no SA were predicted below 42°S during the LGM. The southern limits of the PGD for both species reach the Huincul Fault zone at the northern limit of Patagonia, which corresponds to the transition from temperate to cold climates. *Notiomastodon platensis* and *E. neogeus*

seem to have been more associated with tropical and temperate climates, avoiding the colder and more arid environments of southern South America. Climate change caused the remaining glaciers to retreat to the Andes, expanding available areas with favorable weather conditions, such as Patagonia, and enabling both *E. neogeus* and *N. platensis* to extend their geographic distribution. However, this process coincided with the timing of their extinction and prevented the two species from extending their distribution in search of cooler and arid habitats (Villavicencio et al., 2019).

Our results also support the argument that megamammals occupied exposed continental shelf areas during the LGM. The reduction in SA due to the rise in sea level possibly influenced the distribution of suitable areas for *N. platensis* and *E. neogeus* at the end of the Pleistocene and the beginning of the Holocene.

The SDMs of both species suggested that climatic/environmental variations played a key role in the decreases in their SA during the Pleistocene/Holocene transition, but would not have been enough to drive them to extinction (Hanski, 2005). Although these decreases appear to be small, the negative effect of any habitat loss is higher for herbivore mammals with large body mass (body mass estimation for *E. neogeus* is 250 kg, Fariña et al., 2014; and for *N. platensis* is 4,500 kg, Larramendi, 2015), because these losses tend to reduce resource availability (Lino et al., 2019), consequently leading to extinction. Additionally, considering the largest SA, the climatic and environmental/biome changes may only have affected the population densities of *E. neogeus* and *N. platensis*, whereas the qualitative changes in the biomes may have had a greater effect on these species. The climate in the larger SA changed from cold and dry during the LGM to warmer and more humid during the middle Holocene.

Although the geographic distributions of *E. neogeus* and *N. platensis* were similar, their potential distributions were different. In addition to climate change, there was a rapid and considerable modification in the vegetation of the SA, with a rise in dense forests favored by the increases in humidity and temperature during the LGM, and a reduction in open plain habitats, as shown in the survey of past vegetation in this study. Because it had a grazer feeding habit, *E. neogeus* may have been strongly affected by these vegetation changes due to the reduction of pastures (Sánchez et al., 2004; MacFadden, 2005; Semprebon et al., 2016). Sánchez et al. (2006) suggested that late Pleistocene populations of *E. neogeus* might have adapted to a more selective diet, which restricted its occurrence to certain habitats. This change in diet may explain the greater post-LGM reduction in SA for *E. neogeus*. Conversely, *N. platensis* had an opportunistic/generalist diet, feeding on grasses (Mothé et al., 2017a), branches, and other types of vegetation, and thus more access to a wide variety of food resources, which may explain the highly subtle reduction in its SA.

Thus, the changes in climatic conditions modified the habitats of *E. neogeus* and *N. platensis* and played a significant role in their extinction. Although climatic changes were relevant to both megamammals' extinction, we cannot discard a more complex scenario wherein other causes (i.e., human impact, pathologies, etc.), working in synergy, could also explain megafauna extinction in South America.

CONCLUSIONS

Species distribution models revealed similar distribution patterns for *E. neogeus* and *N. platensis* during the last glacial maximum,

but their ecological niches differed mainly in their diet composition, with *E. neogeus* being a grazer and *N. platensis* being an opportunistic/generalist mixed feeder. During the LGM, both species occupied mainly arid and semi-arid open habitats in South America. The total areas suitable for survival decreased after the LGM, suggesting that climatic/environmental changes would have affected *E. neogeus* and *N. platensis* populations during the late Pleistocene. Subsequently, the climate in the suitable areas for both species changed from drier and colder in the LGM to more humid and warmer in the middle Holocene. Thus, climatic and environmental changes in South America were an underlying factor that drove these megamammals to extinction.

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