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RESEARCH ARTICLE

Did the climate changes cause the extinction of the Late Pleistocene gomphotheres in South America?

Evelyn N.S. Cruz[1,2], Søren Faurby[3,4], and Ricardo J. Sawaya[5]

[1]*Laboratório de Evolução e Diversidade I, Universidade Federal do ABC. Rua Arcturus 3, 09606-070 São Bernardo do Campo, SP, Brazil.*
[2]*Laboratório de Ecologia e Geociências, Universidade Federal de Sergipe. Avenida Marechal Rondon, 49100-000 São Cristóvão, SE, Brazil.*
[3]*Department of Biological and Environmental Sciences, University of Gothenburg, Gothenburg, Sweden.*
[4]*Gothenburg Global Biodiversity Centre, Gothenburg, Sweden.*
[5]*Centro de Ciências Naturais e Humanas, Universidade Federal do ABC. Rua Arcturus3, 49100-000 São Bernardo do Campo, SP, Brazil.*
Corresponding author: Evelyn Nathália da Silva Cruz (evelynnathaliascruz@gmail.com)

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ABSTRACT. A global wave of megafauna extinctions occurred between 50,000 and 10,000 years ago, impacting numerous large continental mammals that are crucial to ecosystem dynamics. Among these are the gomphotheres, *Cuvieronius hyodon* (Fischer, 1814) and *Notiomastodon platensis* (Ameghino, 1888), two species closely related to modern elephants. *Cuvieronius* migrated from North to South America during the Pleistocene. Both species became extinct between 15,000 and 7,000 years ago. Proposed explanations for these extinctions include hunting by early human populations in South America and climatic fluctuations during the Pleistocene. We tested the climate change hypothesis over the past 120,000 years as a critical factor related to the extinction of South American gomphotheres. Our analysis relied on paleoclimatic models spanning the Last Interglacial (120,000 years before present – YBP), the Last Glacial Maximum (21,000 YBP), the Oldest Dryas (18,000 YBP), the Younger Dryas (13,000 YBP), and the Middle Holocene (6,000 YBP), marking the last known occurrence of the Pleistocene megafauna. Geographic distribution records of both species were mapped using data from the scientific literature and open databases. Subsequently, suitable climatic areas for both species in South America were identified through species distribution model projections across these five paleoclimatic periods. Our models revealed significant fragmentation of suitable areas for both species during these critical events. This fragmentation likely contributed to their extinction, possibly exacerbated by additional factors such as the establishment of early human populations in the continent.

KEYWORDS. Biogeography, Gomphotheriidae, megafauna, paleobiogeography, species distribution model.

INTRODUCTION

Although South America is currently poor in megafauna species, this was not always the case. Until the end of the Pleistocene, the continent had sixty species of megafauna, following the threshold of 44 kg used by Barnosky (2008). This included saber-toothed felids *Smilodon populator* Lund, 1842 (Felidae), a rich diversity of ground sloths (Megatheriidae, Megalonychidae, Mylodontidae, and Nothrotheriidae; Fernández-Jalvo and Andrews 2016), and at least two species of elephants. During the Late Pleistocene (129,000 to 11,700 years ago) and early Holocene (11,700 to 8,200 years ago), the world suffered an unprecedented magnitude of species extinction (Sandom et al. 2014). This led to the extinction of 52 genera (83%) of South American megafauna and 34 North American genera (72%; Barnosky and Lindsey 2010).

Gomphotheriidae (Fig. 1) is an extinct group of proboscideans closely related to modern elephants (Smith and

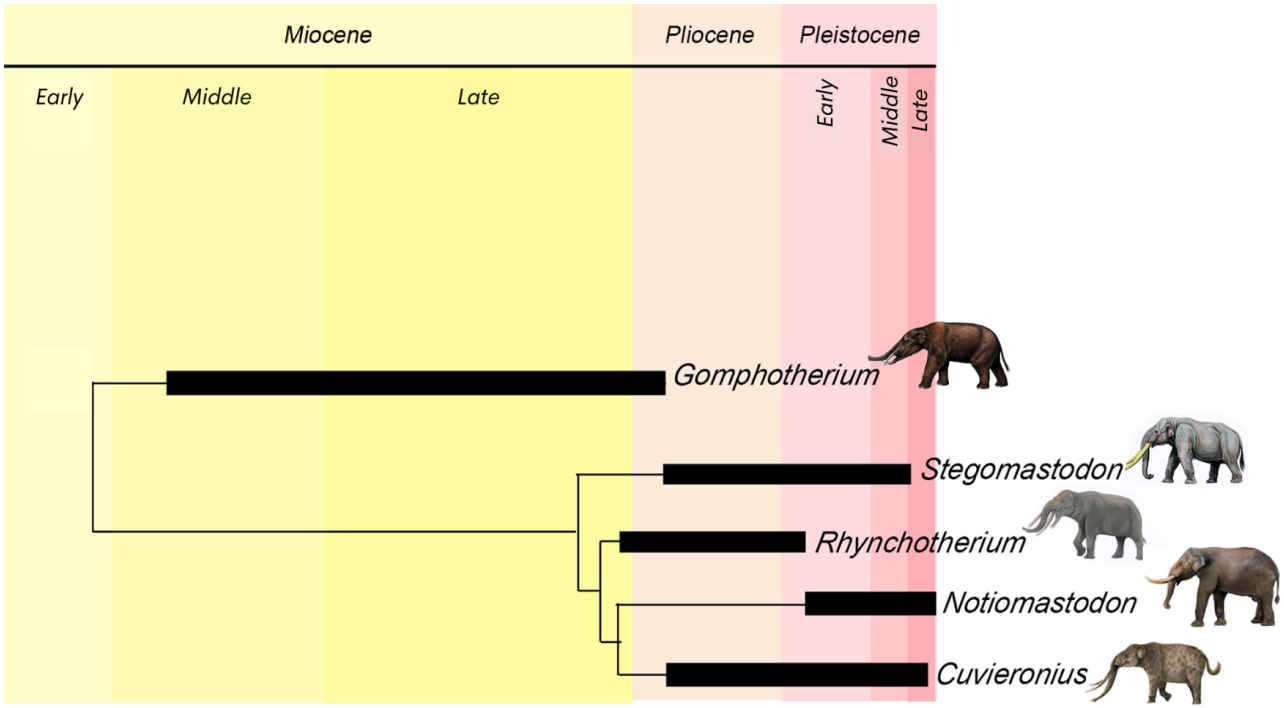

Figure 1. Phylogenetic position of *Cuvieronius* and *Notiomastodon* in Gomphotheriidae. Modified from Smith and DeSantis (2020).

DeSantis 2020), considered paraphyletic (Baleka et al. 2022), includes approximately 13 described genera and around 40 recognized species. Two of these species dispersed across the Americas during the Pleistocene, *Cuvieronius hyodon* (Fischer, 1814) and *Notiomastodon platensis* (Ameghino, 1888). *Cuvieronius hyodon* was distributed across North, Central, and South America, with a significant presence (but not exclusive) in the Andean region of South America. *Notiomastodon platensis* was an endemic species of South America (Mothé and Avilla 2015), with a wide geographical distribution and a diverse diet (Sánchez et al. 2004, Asevedo et al. 2012).

Climate change has driven megafauna migrations over geological time. Molecular studies on American mastodons, *Mammut americanum* (Kerr, 1792), and steppe bison, *Steppe bison* (Bojanus, 1825), have revealed complex relationships between population dynamics and climate variability, particularly during glacial and interglacial transitions, such as the last deglaciation, when population expansions coincided with glacial retreat (Karpinski et al. 2020). These findings support the hypothesis that ongoing warming could lead to significant biogeographical changes.

Pleistocene megafauna experienced major climatic events, including the Last Interglacial (LIG, 130,000–115,000 BP), marked by higher temperatures at high latitudes and a sea level seven meters higher than the current one (Van de Berg et al. 2013). During the Last Glacial Maximum (LGM, 21,000 BP), cooler global temperatures and regional hydrological changes were observed, especially in South America (Cook et al. 2006). While the western Amazon became wetter, the eastern portion experienced drier conditions, reflecting the South American Precipitation Dipole, a pattern linked to orbital precession cycles (Cook et al. 2006, Cheng et al. 2013a).

Subsequent climatic episodes, such as the Oldest Dryas (OD, 18,000 to 14,500 BP) and the Younger Dryas (YD, 12,900 to 11,500 BP), brought further environmental fluctuations. Although its impacts on South America remain unclear, similar environmental changes may have affected the distribution and availability of resources for the megafauna. The Younger Dryas caused a return to glacial conditions, shifting westerly winds southward and producing cooler, drier climates in some areas (McCulloch et al. 2000). These events were succeeded by the onset of the Holocene (11,600 BP) brought rapid warming and intensified monsoon activity in parts of Central and South America, driven by ocean-atmosphere interactions (Harrison et al. 2003, Prado et al. 2015).

Understanding these climatic fluctuations is essential to reconstruct the environmental pressures faced by Pleistocene megafauna. These animals likely struggled with habitat loss and shifting food availability due to rapid ecological changes (Lima-Ribeiro et al. 2013, Araújo et al. 2021). However, while climate was a major factor, it may not fully explain extinction patterns. Comparisons with extant species, such as forest-dwelling ungulates (Galetti 2004), provide useful analogs but remain insufficient to capture the complexity of past ecosystems. Vegetation shifts, potentially driven both by climate and by the decline of large herbivores, such as the Gomphotheriidae, likely played a role in reshaping ecological communities (Daskin et al. 2016).

Climate changes alone could have exterminated the megafauna (e.g., Ficcarelli et al. 2003, Sandom et al. 2014). However, only abrupt and severe shifts would likely have been sufficient, possibly in combination with other stressors such as habitat modification and human activity (Barnosky et al. 2004, Faith and Surovell 2009). Increased temperature and precipitation may have promoted forest expansion at the expense of open habitats, reducing suitable environments for savanna-adapted species. While some authors dispute a significant human role, archaeological evidence, though limited, suggests that interactions did occur. Sites like Monte Verde (Meltzer 1993) and Pilauco (Moreno et al. 2019) in southern Chile contain faunal remains, plant materials, tools, and even hominin footprints, supporting pre-Clovis human presence and possible overlap with megafauna.

Our study aims to identify climatically suitable areas for two South American gomphothere species during five major climatic events faced by Pleistocene megafauna, notably the Oldest Dryas, Younger Dryas, and the period of the last occurrence of one of the species during the Holocene. Unlike previous studies that have primarily focused on the broad-scale ecological factors influencing extinction, our study specifically examines the role of climate as a potential primary driver of extinction. By incorporating high-resolution climate data and modeling the species' climatic suitability across multiple climatic shifts, our analyses provide a more comprehensive understanding of how climatic changes may have influenced species survival and extinction, offering new insights into South America's Pleistocene megafauna extinction debate.

MATERIAL AND METHODS

Data

Our records were sourced from the Paleobiology Database (McClennen et al. 2024) and relevant literature, including taxonomic revisions of the Gomphotheriidae (e.g., Mothé et al. 2013), and additional sources such as publications on South American Quaternary gomphotheres (e.g., Ossa and Moseley 1972, Falguères et al. 1994, Kinoshita et al. 2005, Gutiérrez et al. 2005, Alberdi et al. 2004, Robles-Camacho 2010, Ribeiro et al. 2013, Dantas et al. 2013a, Dantas et al. 2013b, Dantas et al. 2017, França 2014, Kerber et al. 2011, Dávila 2019). We also consulted literature from various databases, including Google Scholar, focusing on occurrences with clear indications of the period to which the samples were dated, with an emphasis on records from specific periods, such as interglacial stages. A detailed list of occurrences is provided in the Supplementary Table S1. *Cuvieronius hyodon* (n = 34) was mainly distributed in the Andean region of South America during the Last Interglacial (120,000 years before present – YBP), with the southernmost point located in southern Bolivia (Fig. 2). More records were abundant in southern North America and Central America (see Fig. 2). According to the known fossil record, *Notiomastodon platensis* (n = 57) was mainly distributed in Northeastern Brazil, along the Brazilian coast, in the Chaco region of Argentina, and in the Trans-Andean and Caribbean regions of South America (Fig. 2). We found a concentration of points in coastal areas close to the equator on both the east and west coasts of South America (see Fig. 2). Based on these occurrences, we used South America as the modeling background for *Notiomastodon* and all of Latin America for *Cuvieronius*.

Species distribution modeling

Species distribution models (SDMs) were implemented using bioclimatic data derived from paleoclimate estimations and paleoclimatic data within the R software environment (version 4.2.0, R Core Team 2020). The paleoclimatic variables were obtained from the PALEO-PGEM model, emulated and published by Barreto et al. 2023. This dataset was preferred due to its high temporal resolution (1 kyr) and its global spatio-temporal coverage, making it particularly useful for understanding climate dynamics over the last five million years. Additionally, its relevance to studying biodiversity patterns and climate change in South America further supports its selection. Time slices corresponding to significant climatic events, including the Last Interglacial (LIG), Last Glacial Maximum, Older Dryas (OD), Younger Dryas (YD) periods, and 6,000 YBP, were extracted from the dataset. Using a custom R script, we applied the Inverse Distance Weighting (IDW) method to interpolate these data specifically for South America, generating spatially explicit

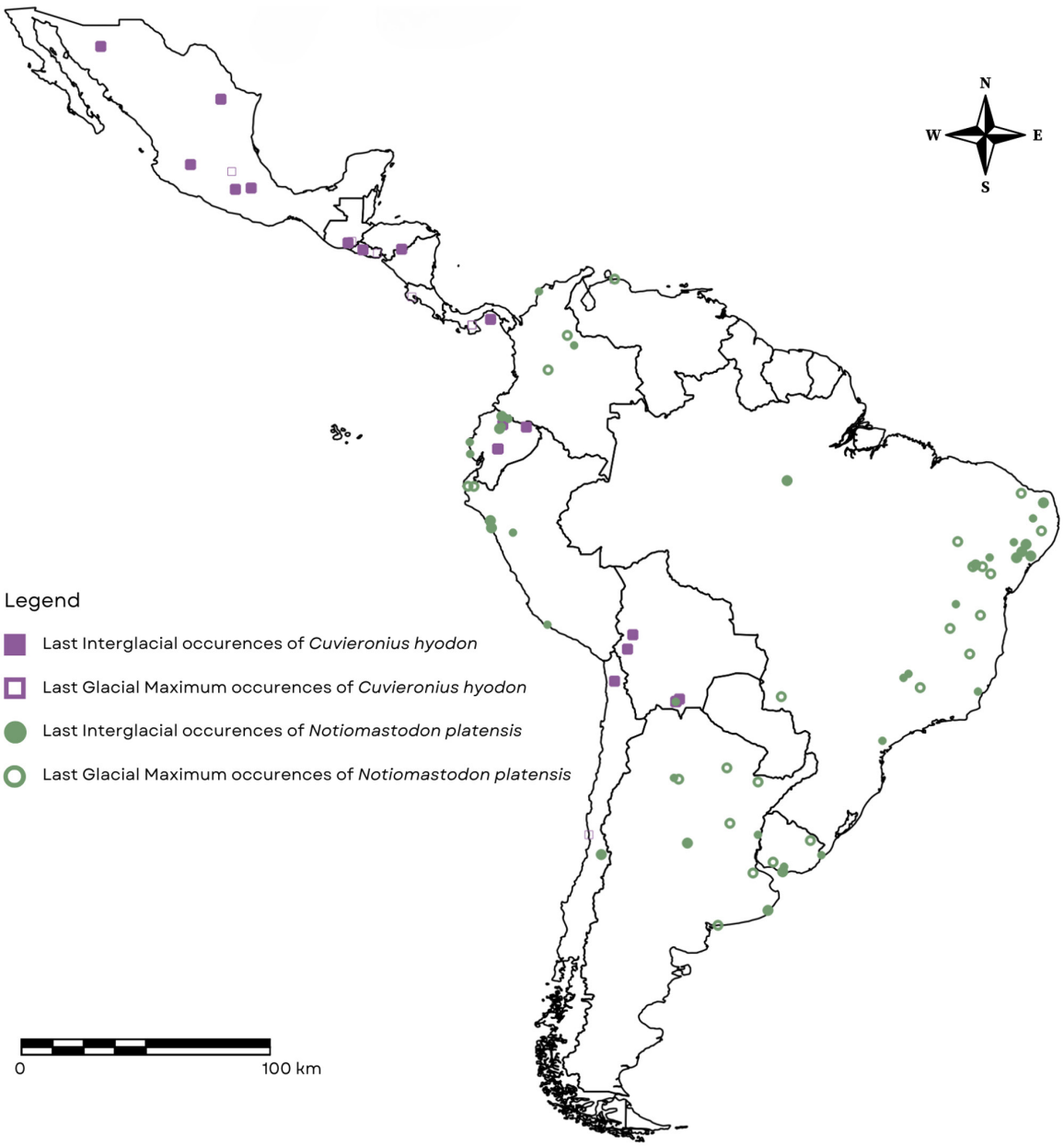

Figure 2. Geographical distribution of *Cuvieronius hyodon* (square) and *Notiomastodon platensis* (circle) during the Last Interglacial (120,000 years before present), Last Glacial Maximum (21,000 years before present).

climate layers. These interpolated climate data were saved as TIFF files and used for species distribution modeling.

Initially, 17 climatic variables were considered for model selection. Given the number of species occurrences available (as discussed in the next section), a maximum of five variables could be retained to avoid overfitting. To assess multicollinearity, Variance Inflation Factors (VIF) were calculated using the USDM package (Naimi 2017). Four variables with low VIF values were selected for further analysis: Annual Mean Temperature (BIO1), Minimum Temperature of Coldest Month (BIO6), Temperature Annual Range (BIO7), and Precipitation of Coldest Quarter (BIO19).

A subsequent step involved evaluating collinearity among these variables. After this evaluation, the final se-

lection for *Notiomastodon* included BIO1, BIO7, and BIO19, while for *Cuvieronius*, only BIO1 and BIO7 were retained. The selection of these variables reflects the distinct ecological preferences of each species. For *Notiomastodon*, the inclusion of both temperature and precipitation variables (BIO1, BIO7, and BIO19) was based on its broader climatic requirements, while *Cuvieronius* was modeled using only temperature-related variables (BIO1 and BIO7), likely reflecting a more temperature-driven habitat preference. Among the variables that did not show spatial autocorrelation, BIO19 was the only one that involved precipitation, despite being combined with temperature data.

For *N. platensis*, models were trained using 39 occurrence records from the LGM period (21,000 Ybp). Similarly, *C. hyodon*'s models were based on 19 occurrence records from the LIG period (120,000 YBP). The selection of these periods for model training was based on the availability of the highest number of occurrence records. To reduce spatial bias, a spatial thinning procedure was applied, and duplicate occurrence records were removed using the spThin package (Aiello-Lammens et al. 2015). A Mantel test was performed to assess spatial autocorrelation among the selected non-collinear predictor variables, with functions from the ecodist (Goslee and Urban 2017) and ecospat (Broennimann et al. 2016) packages, ensuring a minimum distance of 55 km between points. We generated 10 models using a bootstrap approach for each species, for each variable, in each period, and our final model represents a consensus among them.

The SDMs were developed using the SDM package (Naimi and Araújo 2016), employing Generalized Additive Models (GAM), Random Forest (RF), and Boosted Regression Trees (BRT). These algorithms were chosen for their ability to capture non-linear relationships and complex interactions between environmental predictors and species distributions. While simpler models may reduce uncertainties when projecting distributions across different periods (Merow et al. 2014), the complexity of the studied species' ecological niches and the variability inherent in paleoclimatic data warranted the use of these algorithms.

To address concerns regarding model transferability, we implemented stringent evaluation metrics, including the Area Under the Curve (AUC, Bradley 1997) and the True Skill Statistic (TSS, Allouche et al. 2006), both ranging from 0 to 1. For TSS, values between 0.60 and 0.90 indicate fair to good model performance, with values closer to 1 reflecting a higher degree of agreement (Allouche et al. 2006). For AUC, a threshold above 0.7 is considered indicative of acceptable accuracy in species modeling (Raes and Ter Steege 2007). Additionally, ensemble modeling was used to mitigate variability and improve reliability in projections. This approach allowed us to balance ecological complexity with robust evaluation, ensuring meaningful predictions while acknowledging the trade-offs associated with algorithm selection.

The modeling focused on the specific climatic periods mentioned earlier, generating predictive maps based on the species distributions predicted by the trained SDMs. These models were designed for the climatic periods of interest and then binarized. A threshold was established based on balanced sensitivity and specificity (sp = se) to create binary presence-absence maps for each species. Sensitivity represents the true presence rate, minimizing omission errors. On the other hand, specificity shows the proportion of true absences predicted to reduce commission or over-prediction errors. Thus, this metric defines the threshold for occurrence probabilities that balances omission and commission errors (Fielding and Bell 1997, Giannini et al. 2012). Finally, we produced response curves for each climatic variable's effect on species suitability and employed the raster function to calculate the proportion of suitable pixels across the South American territory.

RESULTS

The occurrence records indicate the presence of *N. platensis* in Colombia, Ecuador, Peru, Chile, Argentina, Uruguay, and Brazil during the Pleistocene, while *C. hyodon* was recorded in Mexico, El Salvador, Honduras, Nicaragua, Panama, Ecuador, Bolivia, and Chile during the same period. Additionally, the climatic suitability for *C. hyodon* extended beyond these occurrence areas to Guyana, Suriname, French Guiana, Colombia, Venezuela, Peru, Paraguay, Argentina, and Brazil, while for *N. platensis*, it expanded to Guyana, Suriname, French Guiana, Bolivia, and Paraguay.

All models were well evaluated, with AUC values greater than 0.79 (GAM; Table 1) and TSS greater than 0.65 (GAM; Table 1). The response curves to climatic variables (Fig. 3) revealed that *C. hyodon* showed higher climatic suitability at annual temperatures (BIO 1) around 15 °C and in more stable climates, with lower annual temperature variation (BIO 7). In contrast, the climatic suitability of *N. platensis* is more responsive to lower precipitation (BIO 19), with optimal intermediate values for annual temperature means (BIO 1) and annual temperature variation (BIO 7; Table 1, Fig. 3).

The SDMs generated for *C. hyodon* (Fig. 4A) and *N. platensis* (Fig. 4B) exhibit differences in climatic suitability variation across the five analyzed periods. This variation is

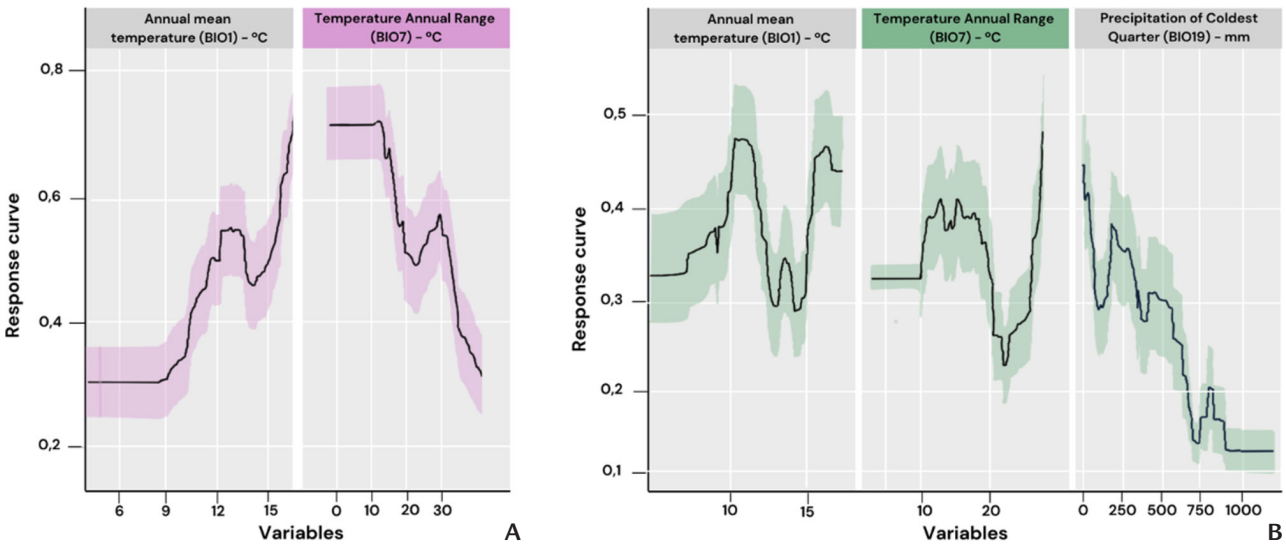

Figure 3. Climate suitability response curves for *Cuvieronius hyodon* (A) and *Notiomastodon platensis* (B) for each of the modeled climatic variables.

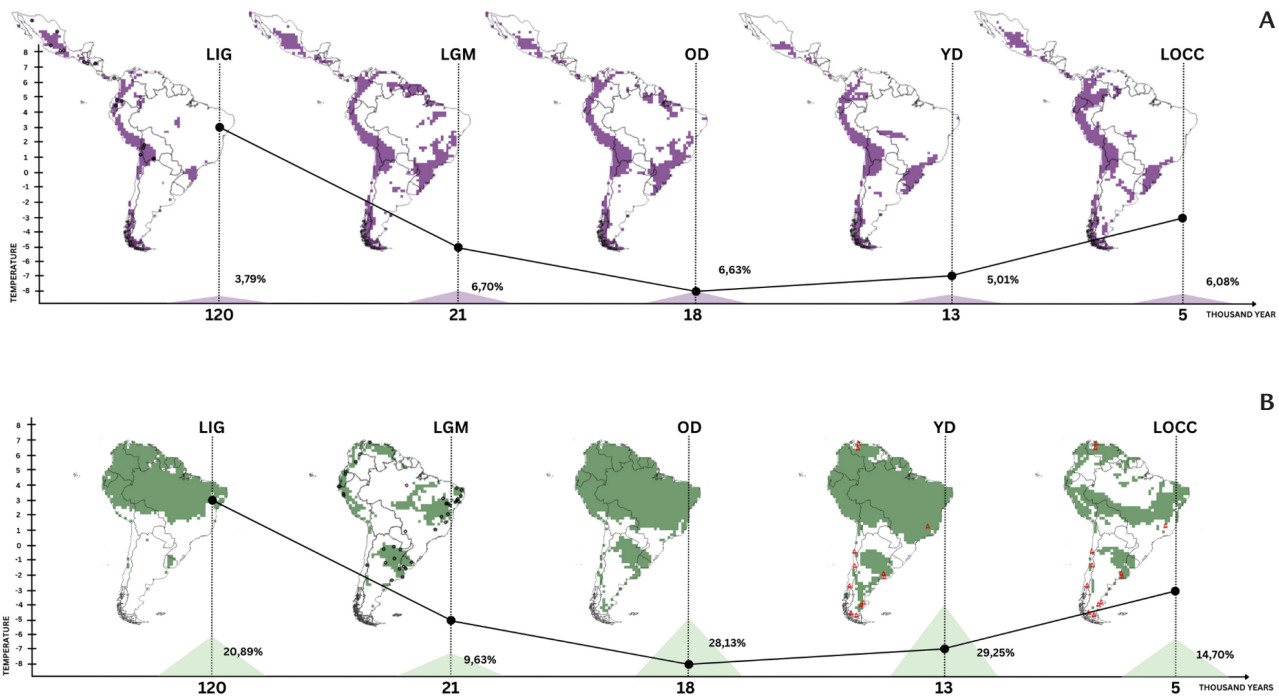

Figure 4. Predicted climatic suitability for *Cuvieronius hyodon* (A) and *Notiomastodon platensis* (B) in the following periods: Last Interglacial (LIG, 120,000 YBP), Last Glacial Maximum (LGM, 21,000 YBP), Oldest Dryas (OD, 18,000 YBP), Younger Dryas (YD, 13,000 YBP), and following the last occurrence of megafauna in South America (LOCC, 5,000 YBP). The black line represents temperature variation across these periods – Source: Vostok station ice core data, Antarctica, from Arruda and Schaefer (2020). The percentages highlighted with triangles in each period indicate the proportion of suitable area relative to the total area of South America. In the models for *N. platensis* for the YD and LOCC periods, occurrences of evidence for human-megafauna interaction on the continent are highlighted in red, according to the Killsite Database (Bampi et al. 2023).

Table 1. Contribution of each variable to the models generated for *N. platensis* and *C. hyodon*, and evaluation of the Random Forest (RF), Generalized Additive Models (GAM), and Boosted Regression Trees (BRT) using the metrics Area Under the Curve (AUC) and True Skill Statistic (TSS) for both species. (Tavgi) Average temperature for each month, (PPT) Total monthly precipitation.

Predictor	Formula	Variable importance (N = 10 replicates)		
			N. platensis	*C. hyodon*
BIO 1 - Annual mean temperature	$Bio\,1 = \frac{\sum_{12}^{1} Tavgi}{12}$			
Average percentage of the variable for the sum of the models			15.90%	57.80%
BIO 7 - Temperature annual range	$Bio\,7 = Bio\,5 - Bio\,6$			
Average percentage of the variable for the sum of the models			20.50%	25.70%
BIO 19 - Precipitation of the coldest quarter	$Bio\,19 = \sum_{12}^{1} PPTi$			
Average percentage of the variable for the sum of the models			27.90%	
Evaluation metrics		Algorithm	*N. platensis*	*C. hyodon*
AUC		Random forest	0.90	0,88
TSS			0.82	0.78
AUC		GAM	0.88	0.79
TSS			0.74	0.65
AUC		BRT	0.93	0.82
TSS			0.84	0.68

considerable only for *N. platensis*, reflecting the influence of past climatic fluctuations on its potential distribution. In contrast, *C. hyodon* shows more stable areas over time, particularly in the central and northern Andes, where the models indicate relatively stable climatic suitability. This suggests that these regions may have served as potential refugia for *C. hyodon* during periods of climatic instability, reinforcing its association with more stable environments. The variables that contributed most to the climatic models were BIO 1 (57.80%) for *C. hyodon* and BIO 19 (27.90%) for *N. platensis* (Table 1).

We quantified the percentage of suitable habitat relative to the total land area of South America (Fig. 4) for both species. For *C. hyodon*, we observed an average of 5.62% of suitable area across different periods (LIG = 3.79%; LGM = 6.70%; OD = 6.53%; YD = 5.01%; LOCC = 6.08%), with the highest suitability during the LGM. On the other hand, *N. platensis* showed a significantly higher average of 20.5% (LIG = 20.89%; LGM = 9.53%; OD = 28.13%; YD = 29.25%; LOCC = 14.70%), indicating a broader distribution of suitable habitats throughout the periods considered. These variations highlight how the available ecological niches for each species changed over time and how climatic conditions influenced their spatial distribution across the continent.

In the SDMs generated for the Younger Dryas and the period following the last occurrence of megafauna in South America (LOCC), we highlight areas where evidence of human-megafauna interaction has been documented, based on the Killsite Database. However, this overlap was only considered for *N. platensis*, as there are no confirmed records of *C. hyodon* in South American paleoarchaeological sites. The absence of *C. hyodon* in such contexts suggests either a lack of direct human exploitation or preservation biases that may have influenced the fossil record. This difference in documented human interactions may also reflect distinct ecological or behavioral traits between the two taxa, such as habitat preferences or migratory patterns, which could have influenced their likelihood of encountering human populations.

DISCUSSION

We reject the Pleistocene climate change hypothesis as the main factor related to the extinction of both species in the Americas based on the geographical distribution patterns of South American gomphotheres. Our results show that *N. platensis* occurred primarily in the Brazilian Shield, encompassing regions such as the Atlantic Forest, Caatinga in northeastern Brazil, Chaco in northern Argentina, and the Pampas. Fluctuations in its range, including its disappearance and reappearance in the Amazon and Chaco regions, suggest significant climatic disturbances that could have contributed to local extinctions. These findings imply that climate may not have been the primary driver of extinction, but rather, disturbances that led to changes in local habitats. In contrast, *C.*

hyodon experienced a more stable climate, occurring primarily in the Andean region of North America, Central America, and western South America. While our analysis showed overlap in suitable areas for both gomphothere species, competition for resources is unlikely due to the distinct altitudes inhabited by each species, as discussed in studies on the geographic distribution and ecological requirements of *Cuvieronius* and *Notiomastodon* (Alberdi et al. 2008, Mothé et al. 2017). Notably, there are records of *C. hyodon* in the lowlands of Peru, contradicting earlier assumptions of a strict Andean distribution (Alberdi et al. 2008, Mothé et al. 2017). Despite the persistence of climatically suitable areas throughout these periods, species extinction could still occur if individuals were unable to disperse and track these regions, particularly in scenarios where habitat fragmentation restricted movement.

Last Interglacial and Last Glacial Maximum

We observed the smallest suitable area for *C. hyodon* during the warmer interglacial period (LIG). Subsequently, during the Last Glacial Maximum, there was an expansion of climatically suitable areas (Fig. 4A). This expansion could be explained by the cooler and moister environments, which are more suitable for this species, as well as the expansion of more closed vegetation areas, particularly in regions with abundant C3 plants, such as the Andean highlands. These conditions suggest that *C. hyodon* adapted to environments with higher humidity, which were more prevalent in the highlands of Bolivia, Chile, Ecuador, and Peru during the LGM. Studies by Wang et al. (2004) and Cruz et al. (2005) further support this by indicating that southeastern Brazil, parts of the Andes, and coastal areas received more moisture during the LGM, aligning with the species' preference for forested habitats. Despite the increase in temperature from the Last Glacial Maximum to the Middle Holocene, where we have the last occurrence of megafauna recorded, large climatically suitable areas for this species can still be observed, especially in the Andean region and southwestern South America (Fig. 4A). Throughout the five time periods, the Andean region maintained the lowest minimum temperature values in South America, likely influencing the preferential occurrence of *C. hyodon* in this region.

Large fragmentation of suitable areas was observed during the Last Interglacial and the Last Glacial Maximum. This was a substantial factor indicated for the extinction risk of Eurasian megafauna (Mondanaro et al. 2021), with approximately 38% importance, followed by other variables such as dietary preferences. However, during the Last Glacial Maximum, we recovered a concentration of occurrence records (Fig. 2), as well as a large block of suitable areas in northeastern Brazil (Fig. 4B). Regarding climatically suitable areas, we observed a 2.91% increase for *C. hyodon* (Fig. 4A), suggesting that this species may have benefitted from environmental conditions during the period under consideration, possibly due to its adaptability to slight climate fluctuations. On the other hand, *N. platensis* experienced an 11.26% decrease in suitable areas (Fig. 4B), indicating a contraction of its viable habitat. This decline could be attributed to the reduced availability of optimal conditions for the species, which may have been more sensitive to the environmental changes occurring at that time, such as temperature shifts and precipitation patterns. These shifts in the spatial distribution of suitable areas are crucial in understanding the ecological pressures faced by these species and may have contributed to their differing responses during the climatic transitions of the Last Glacial Maximum.

Interpretations of the paleoenvironmental conditions of this northeastern semiarid region allow us to infer that the Caatinga oscillated towards savannas capable of maintaining the Pleistocene megafauna, probably maintaining low rainfall during these periods. De Vivo and Carmignotto (2004) defend the idea that the Pleistocene megafauna went extinct in a scenario with 50% more rain than the present, transforming open areas into extremely dense and closed vegetation areas, difficult to access, with decreasing migrations, when these animals must have become extinct.

Notiomastodon platensis was also mainly affected by the precipitation of the coldest quarter (BIO 19) was an important predictor variable in the models (Table 1), with greater suitability in areas with lower precipitation, preferring warmer and drier conditions. During these glacial cycles, much of the continent was also relatively drier. However, some still humid regions must have favored the expansion of forests, including the Amazon, with rainfall greater than 750 mm, and the southern Atlantic Forest, an area with the highest rainfall values on the continent (Cheng et al. 2013b). Forest-dwelling megafauna are likely underrepresented in the fossil record due to poor preservation in humid tropical forests. There is isotopic evidence that several of the extinct megafauna were browsers, which could plausibly find food in forested environments (Doughty et al. 2013), and extant proboscideans are also regularly found in forests.

From the Dryas until extinction

These two events have been less explored in the overall context of South America so far. However, some studies conducted in Argentina present interesting results that

merit discussion regarding their impact on the extinction of Pleistocene megafauna. In the Northern Hemisphere, the transition from the Last Glacial Maximum to the Holocene is characterized by rapid cooling followed by a pulse of rapid warming. However, palynological data indicate that this event occurred 400 years earlier in the Southern Hemisphere (Kröhling and Iriondo 1999, Hajdas et al. 2003, Prado et al. 2015).

For *Cuvieronius*, the suitability between events and the percentage of suitable areas remained almost constant since the Last Glacial Maximum, with notable area losses in northeastern Brazil during the Younger Dryas (Fig. 4A). The region remained climatically stable for the establishment and persistence of this species, but it may have faced additional pressures during the Younger Dryas. In the Pampas, for instance, sediments contain ichnofossils of extinct megamammals dated to 12,000 YBP, suggesting that the sea level drop may correspond to the Younger Dryas (Prado et al. 2015). During the early Holocene, extensive areas of the exposed continental shelf east of the Pampas coastline were gradually inundated (Prado et al. 2015). Proxy data indicate that eolian deposition ceased at the beginning of the Holocene, with soil development and the presence of temporary ponds indicating a transition to more stable climatic conditions (Prado et al. 2015).

Our models indicate only 1% of increase in climatically suitable areas for *Cuvieronius* between the Younger Dryas and the Holocene. Overall, there are no significant percentage variations in suitability across the models, and the Andes Mountains appear to have acted as a climatic refuge for the species. However, as discussed by Mothe et al. (2022), these updated geographic distributions challenge the previously proposed migratory routes for South American proboscideans. While it was once thought that *Notiomastodon* followed the 'Eastern Savanna' path and *Cuvieronius* spread into South America via the 'Andean corridor' (Prado et al. 2005, Mothé et al. 2012), recent evidence suggests that the inter-Andean valleys, such as the Cauca Valley, could have provided suitable conditions for both species, supporting their dispersion through the Andean mountains. Climatic fluctuations and vegetation shift during the Last Glacial Maximum likely influenced their distribution, with dry and montane forests in the inter-Andean valleys offering a dry corridor for their movement (Hooghiemstra and Flantua 2019, Jaramillo et al. 2022). Additionally, no archaeological sites have been described for this location so far, suggesting that the extinction of *Cuvieronius* may have faced pressures beyond climate and hunting.

In contrast, models generated for *Notiomastodon* indicate a reduction of over 50% in suitable areas during these periods. The reduction in suitable areas between the glacial maximum and the Holocene has previously been identified for *N. platensis* in earlier studies (Araujo et al. 2021), where the consequent habitat changes caused by this factor are pointed out as playing a significant role in their extinction. This is due to the shift from the dry and cold conditions experienced since the LGM (maintained during the Older Dryas and Younger Dryas) to the warm and humid conditions of the Holocene.

The climate hypothesis

In the Middle Holocene, when *C. hyodon* and *N. platensis* likely became extinct, large areas would still be climatically suitable for the persistence of both species of gomphotheres, as predicted by species distribution models (Figs 4A, 4B). Human migrations into North, Central, and South America have been proposed as an alternative hypothesis for megafauna mass extinctions on the continent (Pratez and Peres 2021). The drivers of the global Quaternary megafaunal extinction are constantly being updated and discussed. So far, there is only one known fossil site in Brazil showing evidence of hunting *N. platensis*, as described by Mothé et al. 2020. For South America, the Kill Site Database (Bampi et al. 2023) provides robust and reliable information with empirical evidence of human-megafauna exploitation during the late Quaternary. These sites overlap with areas suitable for *Notiomastodon* (Fig. 4A). However, there are no recorded occurrences of *Cuvieronius* overlapping these archaeological sites (Fig. 4B). Therefore, even if these species did not go extinct primarily due to the fragmentation of suitable areas or population vulnerability caused by major climatic changes, they might have faced additional extinction pressure from the first Paleoindian populations on the continent. However, due to the lack of data on the frequency of their occurrences, it is not possible to directly test the hypothesis of population decline.

When we compare the South American and North American extinctions, there are some inconsistencies related to the climate extinction hypothesis. Changes in climate and vegetation were not synchronized across continents. The southern tip of South America gradually warmed, while the Northern Hemisphere experienced abrupt warming at 14,700 YBP. Meanwhile, southern South America felt the effects of relatively minor cooling (Antarctic Cold Reversal) (Blunier et al. 1997, Fiedel and Haynes 2004).

The presence of early Paleoindian populations in North America dates to during and immediately after the

Last Glacial Maximum (approximately 26,500–19,000 YBP), but broader occupation occurred from a period of abrupt warming (Becerra-Valdivia and Higham 2020). In this case, widespread expansion was a key factor in the extinction of large terrestrial mammals (Becerra-Valdivia and Higham 2020), likely due not only to hunting—already well documented at several sites, but also to the increasing overlap and competition for resources between humans and megafauna. However, it is important to note that some taxa, such as *Cuvieronius*, have not been recorded at archaeological sites in South America, suggesting that human interaction was not a universal extinction mechanism for all species across the continent. The absence of *C. hyodon* in such contexts suggests either a lack of direct human exploitation or preservation biases that may have influenced the fossil record.

Hunting is considered to have played a significant role in the extinction of South American megafauna. Evidence suggests that widespread hunting by Paleo-Indians led to a substantial decline in megaherbivore populations, particularly in regions with low population densities (Brook and Bowman 2004, Barnosky et al. 2016). These areas were more vulnerable to local extinctions due to combined pressures from human activities and stochastic environmental factors (Galetti 2004, Sandom et al. 2014). The reduction in megafaunal populations likely disrupted ecological networks, further accelerating extinction processes (Malhi et al. 2016). Future studies should further explore the synergistic effects of climate change and human impact on these extinctions.

Final remarks

Different climatic variables may have influenced the geographical distribution of South American gomphotheres, but not their extinction. *Cuvieronius hyodon* likely benefited more from low temperatures, whereas *N. platensis* was more influenced by lower rainfall. Our results reject the climatic hypothesis for their extinction, based on species distribution models.

While climate shaped the habitats and ranges of these species, it was not the primary driver of their disappearance. The persistence of climatically suitable areas throughout glacial and interglacial periods suggests that other factors contributed to their extinction, with human activity being a plausible cause. The timing of early human migration into the Americas and evidence of human–megafauna interactions, such as hunting, align with declines in gomphothere populations, indicating that anthropogenic pressures were likely critical.

The overlap of human activity with suitable habitats implies that habitat fragmentation, hunting, and potential competition for resources may have synergistically accelerated their decline. Future research should integrate paleontological and archaeological data to clarify the role of humans in megafaunal extinctions. A multidisciplinary approach will better elucidate the complex interactions between climate, human activity, and megafauna survival.

Although climate influenced the distribution of *C. hyodon* and *N. platensis*, human activities—particularly hunting and habitat alteration—likely played a more significant role in the decline of these iconic South American megafauna.

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Supplementary material 1

Table S1. Occurrence data used for species distribution modeling (SDM), including species name, geographical coordinates (Lat, Long), collection ID or deposit location (Collection ID/deposit locat), specific location, approximate period, source of occurrence (Source), and reference.

Authors: Evelyn N.S. Cruz

Data type: Database.

Link: https://doi.org/10.1590/S1984-4689.v42.e24051

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Author Contributions

ENSC: Conceptualization, Writing original draft, Formal Analysis. SF: Conceptualization, Methodology, Writing - review & editing. RJS: Project administration, Conceptualization, Methodology, Writing - review & editing, Resources.

Competing Interests

The authors have declared that no competing interests exist.

Data Availability

Datasets generated or analyzed in this study are available from the corresponding author on reasonable request.

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