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Research article

Evaluating migration hypotheses for the extinct *Glyptotherium* using ecological niche modeling

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Ecography
2025: e07499
doi: 10.1111/ecog.07499
Subject Editor:
Manuel J. Steinbauer
Editor-in-Chief: Miguel Araújo
Accepted 2 December 2024

The formation of the Isthmus of Panama allowed for migrations between the once separated continents of North and South America. This led to one of the greatest documented interchanges of biota in Earth history, wherein an array of species across many groups migrated between the continents. *Glyptotherium*, a giant extinct armadillo-like grazer, is an example of a taxon that likely originated in South America and migrated to North America. Here we use Ecological niche modeling to test the extent of suitable conditions for *Glyptotherium* in Central America and surrounding regions during the intervals when the taxon is thought to have dispersed, allowing for assessment of plausible migration routes and the hypothesis that the genus migrated from North America back to South America during the Rancholabrean (14 000–240 000 years ago). Our niche modeling results show suitable abiotic conditions for *Glyptotherium* in Central America and the surrounding area throughout the Plio-Pleistocene, with western South America (the 'high road') suggested as their ancestors' route northwards. Depending on the extent of suitable conditions, it may have been possible for *Glyptotherium* to return to South America during the Rancholabrean. The results support previous hypotheses that the range of *Glyptotherium* was constrained by the need for warm, wet environments.

Keywords: *Glyptotherium*, Great American Biotic Interchange, migration, niche modeling

Introduction

The formation of the Isthmus of Panama enabled a series of migrations and subsequent diversification and extinction events that shaped the late Neogene terrestrial faunas of

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North and South America. The timing of the emergence of the Isthmus is controversial, with hypotheses ranging from 23 to 2.5 Ma ago (Bacon et al. 2015, Montes et al. 2015, O'Dea et al. 2016, Jaramillo et al. 2017), although the final permanent connection probably occurred closer to 2.5 Ma ago (O'Dea et al. 2016). Prior to this connection, North and South America were separated for much of the Cenozoic. North America had been connected to Eurasia at intervals since the Cretaceous (Marincovich and Gladenkov 1999), while the South American fauna developed in relative isolation over the previous 50 million years (Leigh et al. 2014), with the arrival of primates and rodents being notable exceptions (Antoine et al. 2012, Bond et al. 2015, Marivaux et al. 2023).

One of the earliest mammalian dispersers between North and South America, the South American megalonychid sloths, appear in the Greater Antilles as early as 17 Ma ago (MacPhee and Iturralde-Vinent 1994, McAfee and Rimoli 2019) and in North America around 9 Ma ago (Morgan 2008). The appearance in the Greater Antilles suggests either island hopping, by swimming or rafting (Carranza-Castañeda and Miller 2004), or dispersal over a land bridge, known as GAARlandia (MacPhee and Iturralde-Vinent 1994, Agnolin et al. 2019), although the latter hypothesis has been called in to question (Ali and Hedges 2021). By approximately 2.6 Ma ago, dispersal of mammalian groups in both directions accelerated (O'Dea et al. 2016). These dispersal events, termed the Great American Biotic Interchange (GABI), included birds (Weir et al. 2009, Smith and Klicka 2010), insects (Winston et al. 2017), reptiles and amphibians (Vanzolini and Heyer 1985), and freshwater fish (Chakrabarty and Albert 2011). Dispersal is broadly defined as an organism's unidirectional movement away from where they were born or originated (Nathan 2013), whereas, in the case of extant species, migration is the seasonal or annual movement between geographic regions (Rubenstein and Hack 2013). In the paleontological context, migration is defined as a distributional shift of a taxon (Rubenstein and Hack 2013).

For mammalian families, the number of migrations was proportional to the number of families on each of the source continents, so about twice the number of families migrated south than north (Marshall et al 1982). For mammals, about 31% of families and 16% of genera went north, whereas 36% of families and 47% of genera went south (Marshall et al 1982). Simpson (1950) first proposed the idea of a 'Central American filter' – a barrier to dispersal that allowed some taxa to cross and prevented others – to explain why certain taxa did or did not participate in GABI, but he did not discuss the nature of the filter other than to note it was likely ecological. This region is known as the 'Mexican transition zone', in reference to the transition between the Nearctic and Neotropical faunas (Morrone 2020).

The Plio-Pleistocene was a period of global climate change, with transition to a cooler and more arid mean state. Northern Hemisphere glaciations began at approximately 3.6 Ma ago, with ice volume increasing until around 2.4 Ma ago (Mudelsee and Raymo 2005). Glaciations occurred in Patagonia during the same time interval (Clague et al. 2020). During the past five million years, savannas expanded in South America (Domingo et al. 2020, Jaramillo 2023), and this expansion of grasslands may have allowed more taxa, presumably grassland-adapted, to migrate across the Isthmus of Panama (Webb 1978, 1991, Marshall 1988, Vrba 1992). Webb (1978) hypothesized multiple possible migration routes that savanna-adapted organisms could have taken between North and South America: an eastern 'low road' around the Amazon rainforest in South America; a 'high road' through the Andes in South America; and a corridor along the Gulf Coast in North America (Fig. 1). In addition, biogeographers have long recognized rafting on vegetation as a way of colonizing islands (Darlington 1938, Simpson 1940, Censky et al. 1998), and it is possible that rafting through the Caribbean was how some species dispersed between the two continents (Marshall 1988, O'Dea et al. 2016).

Here, we focus on a northward GABI migrant, *Glyptotherium*. The clade Glyptodontinae first appears in the fossil record in northern South America during the Middle Miocene ~12 million years ago (Zurita et al. 2011), and thus *Glyptotherium* is classified as a northward migrant during GABI (Woodburne 2010), even though the genus itself is not known from the Miocene fossil record of South America. We focus on *Glyptotherium* because the genus has diagnostic osteoderms (Zurita et al. 2018), and because fossils of *Glyptotherium* are relatively common in the fossil record (Méndez et al. 2019), given that a single individual possessed ~1800 osteoderms (Gillette and Ray 1981). The genus first appears in the fossil record beginning in Mexico ~3.1–3.9 Ma ago (Flynn et al. 2005), then appears in Arizona ~2.6 Ma ago (Thrasher 2022) and in Florida 1.8–2.7 Ma ago (Morgan 2005), representing the western-most and eastern-most distributional extent of the genus in North America, respectively (Fig. 1; Gillette et al. 2016, Cuadrelli et al. 2023). It is hypothesized that during the Rancholabrean (14 000–240 000 years ago), *Glyptotherium* migrated back into South America (Carlini et al. 2008, Carlini and Zurita 2010, Woodburne 2010), with the southernmost extent of its range in central Brazil (Oliveira et al. 2010, Zurita et al. 2018).

Glyptotherium includes three species: *G. texanum*, *G. cylindricum* and *G. mexicanum* (Ramírez-Cruz and Montellano-Ballesteros 2014, Gillette et al. 2016), although Zurita et al. (2018) propose collapsing the three species into two chronospecies: *G. texanum* and *G. cylindricum*. *Glyptotherium* was living in savanna environments (Pérez-Crespo et al. 2012, Pasani et al. 2019, Omena et al. 2020, Lessa et al. 2021) and is hypothesized to have needed a warm, moist environment for survival (Gillette and Ray 1981, p. 210). To our knowledge, no predictions have been made for the quantitative temperature and precipitation conditions occupied by *Glyptotherium*.

Here, we use ecological niche modeling (ENM) to test how many of the hypothesized climate corridors are plausible for *Glyptotherium*: through the Andes, along the northeast

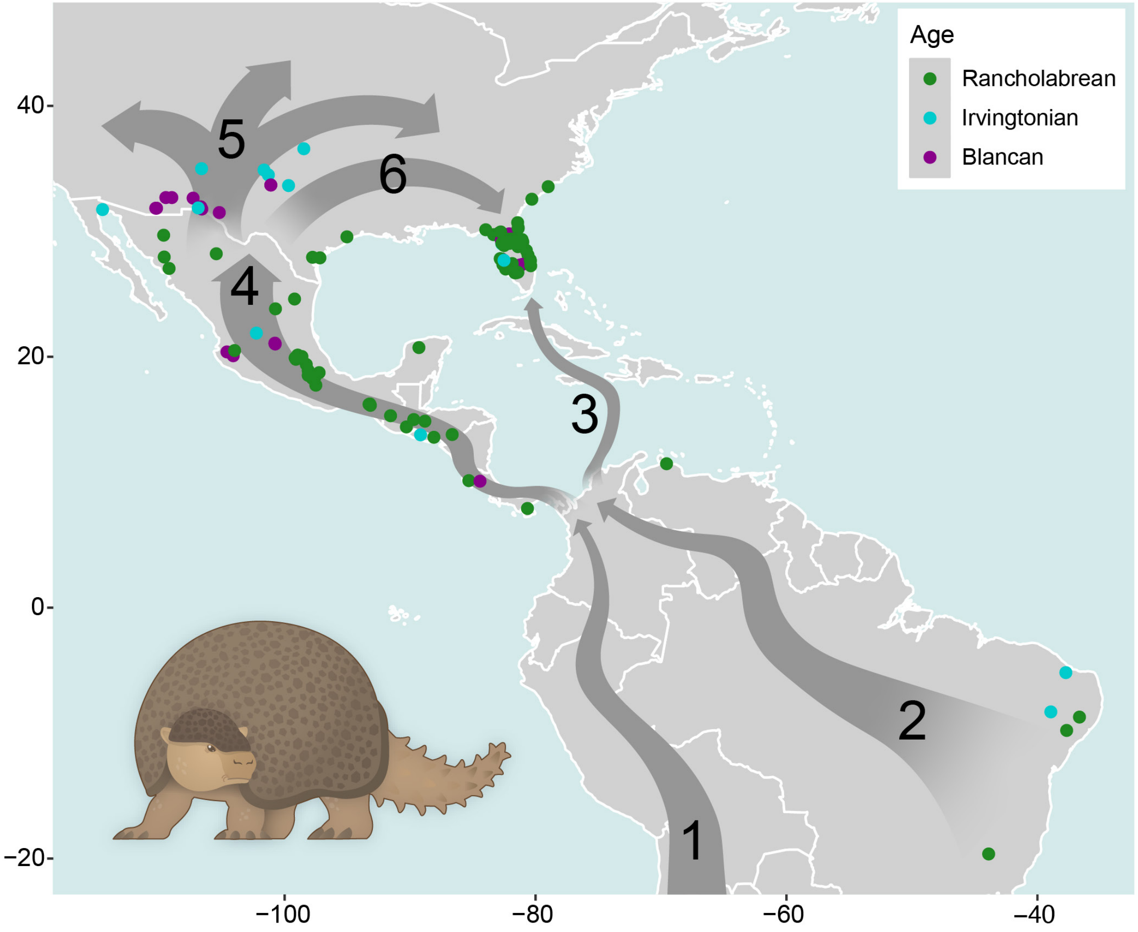

Figure 1. All unfiltered (i.e. not spatially unique) *Glyptotherium* fossil localities used in this analysis, with their approximate ages indicated by the colors: Rancholabrean (0.014–0.240 Ma; green points), n = 85; Irvingtonian (0.240–1.806 Ma; blue points), n = 14; Blancan (1.806–4.75 Ma; purple points), n = 25. Possible migration routes from South America to North America for *Glyptotherium*: the 'high road' through the Andes (1), the 'low road' around the Amazon rainforest (2), or rafting through the Antilles (3). Once through Central America and Mexico (4), *Glyptotherium* could have expanded to the north (5), or stayed in the 'Gulf Coast Savanna Corridor' (6). Figure made in collaboration with Miranta Kouvari (Science Graphic Design). See the Material and methods section for details of the data compilation, and the Supporting information for details on localities.

coast of South America, through Central America, or through the Antilles (Fig. 1). ENMs use species' occurrence data and environmental variables to estimate the suitable conditions for taxa, and these models have previously been applied previously to the fossil record (Svenning et al. 2011, Varela et al. 2011, Saupe et al. 2014, Myers et al. 2015, Blois et al. 2024), including to help investigate paleogeographic ranges of plants (Meseguer et al. 2015, Divíšek et al. 2022), dinosaurs (Chiarenza et al. 2022), and mammals (Maguire and Stigall 2009, Fuentes-Hurtado et al. 2016), among others. Here we use ENM to determine the extent of suitable conditions for the putative savanna-adapted genus *Glyptotherium* in Central America during the time when the taxa dispersed, allowing for the assessment of plausible migration routes, including the hypothesis that the genus migrated from North America back to South America during the Rancholabrean (14 000–240 000 years ago).

Material and methods

Paleoclimate model and environmental variables

We used a recently updated version of the UK Met Office's HadCM3 paleoclimate model (HadCM3L-M2.1D, Valdes et al. 2017) with a resolution of 3.75° longitude (approximately ~300 km in the tropics) and 2.5° latitude for the atmosphere and ocean. This model is described in Valdes et al. (2017) and Valdes et al. (2021). Candidate climate variables used to model suitable conditions for *Glyptotherium* were generated for four time slices: 112 ka ago (boundary between the mid to late Pleistocene), 1.80–2.588 Ma ago (the beginning of the Pleistocene, the Galesian), 2.588–3.60 Ma ago (the late Pliocene, the Piacenzian), and 3.60–5.33 Ma ago (the early Pliocene, the Zanclean). Because we are dealing with the North American terrestrial fossil record, we will refer to these time intervals using their closest equivalent North American Land Mammal Ages (NALMA): the Rancholabrean, the Late Blancan, the Middle Blancan, and the Blancan-Hemphillian, respectively (see the Supporting information for the temporal relationships of the NALMA and the standard international geological timescale). The climatic data were bilinearly interpolated to one degree resolution using the *resample* function in the 'raster' R package ver. 3.6.14 (Hijmans 2023).

Temperature and precipitation have been suggested previously to have been important to *Glyptotherium* (Gillette and Ray 1981) and are also important in constraining plant distributions (Paruelo and Lauenroth 1996, Zhao et al. 2018, Yao et al. 2022), which likely influenced the suitability of migration corridors. We therefore chose annual mean temperature, annual precipitation, minimum temperature of the coldest month, maximum temperature of the warmest month, precipitation of the driest month, and precipitation of the wettest month as our potential climatic predictors for use in the ENMs.

Collinearity among predictor variables in ENM can lead to inaccurate identification of predictors, especially when projecting niche models to new regions or time periods (Dormann et al. 2013, Feng et al. 2019). We therefore tested for collinearity using variance inflation factors (VIFs) with the *vifstep* function in the 'usdm' R package ver. 1.1.18 (Naimi 2017). Predictor variables with a VIF greater than 10 were excluded (Montgomery et al. 2021), which were annual mean temperature and annual precipitation (Supporting information). Thus, the final climate variables used in our ENMs were minimum temperature of the coldest month, maximum temperature of the warmest month, precipitation of the wettest month and precipitation of the driest month.

Fossil locality data

Occurrence data for *Glyptotherium* were obtained from the Global Biodiversity Information Facility (GBIF; accessed 19 August 2021) and the Paleobiology Database (PBDB) (Uhen et al. 2023). These records were supplemented from the literature, primarily concentrating on Central and South America. We identified 17 new records that were entered into the PBDB. We also entered a GBIF record that had not yet been entered into the PBDB. The final access of the PBDB was on 07/18/2023 (Supporting information). After we completed data collection, an additional record of *Glyptotherium* was published (Cuadrelli et al. 2023).

Unfortunately, temporal control for many of the localities was poorly constrained, so we tried to further refine the locality ages using additional chronological data from the literature (e.g. biostratigraphy or radiometric dating). However, typically, the localities could not be assigned with much better precision than the standard North American Land Mammal Ages.

Localities were sorted into four time bins: Rancholabrean (0.014–0.240 Ma) (Sanders et al. 2009, Barnosky et al. 2014), Late Blancan (1.80–2.588 Ma), Middle Blancan (2.588–3.60 Ma), and Blancan-Hemphillian (3.60–5.33 Ma). Occurrence data were rotated to their paleo-coordinates based on their time bin using Scotese's (2016) PaleoAtlas and GPlates ver. 2.3.0 (Müller et al. 2018) for the Rancholabrean (112 ka), Gelasian (2.194 Ma), Piacenzian (3.094 Ma) and Zanclean (4.465 Ma). Any points that fell in the ocean were moved to the nearest cell of land using *points2nearestcell* in the R package 'rSDM' (Rodriguez-Sanchez 2020). Seven points were moved in total (Rancholabrean = 3, Late Blancan = 3, Middle Blancan = 1), the furthest of which was moved 149 km (likely due to the coarseness of our paleoclimate model). Late and Middle Blancan occurrences were filtered to one occurrence per one degree grid cell using the *elimCellDuplicates* function in the package 'enmSdmX' ver. 1.1.6 (Smith 2024). This resulted in 85 Rancholabrean occurrences (prior to spatial filtering), 5 spatially unique Late Blancan occurrences, and 7 spatially unique Middle Blancan occurrences. There were no occurrences in the Blancan-Hemphillian. All remaining analyses were performed in R ver. 4.2.2 (www.r-project.org). Three Brazilian occurrence points were chosen for external validation of model outputs and were therefore set aside before spatial filtering. Rancholabrean occurrences were subsequently filtered spatially at a resolution of 200 km using the *thin* function in 'spThin' ver. 0.2.0 (Aiello-Lammens et al. 2015), resulting in 24 remaining points. Spatial filtering, also known as spatial thinning, helps to accommodate the spatial heterogeneity in occurrence data, which can lead to better-performing ENMs (Pearson et al. 2007, Veloz 2009). Detailed locality and temporal data, along with references, are included in the Supporting information.

Ecological niche modeling

Given the paucity of data for the other intervals, we only built an ENM model in the Rancholabrean (n = 24 after spatially filtering, see above). We modeled environmental suitability using MaxEnt ver. 3.4 (Phillips et al. 2017). MaxEnt is a machine learning presence-only algorithm that estimates suitable environmental conditions by minimizing the entropy in covariate space (Elith et al. 2011). The method has shown good predictive capabilities when compared to other algorithms (Elith et al. 2006, Guisan et al. 2007, Peterson et al. 2007, Merow et al. 2013, Valavi et al. 2022) and performs well with relatively few presence records (Elith et al. 2006, Hernandez et al. 2006, 2008), which characterizes our study system. MaxEnt compares the input localities for the taxon of interest to a sample of background points (Phillips and Dudík 2008, Merow et al. 2013, Whitford et al. 2024). These background points provide information about the range of environmental conditions that are available to the taxon of interest (Phillips et al. 2009, VanDerWal et al. 2009). We defined our calibration region, the area from which background points were sampled, as the region from each occurrence point with an assigned 1500 km radius (circular buffer; approximately 15°), calculated using the *buffer* and *aggregate* functions in the 'raster' R package ver. 3.6.14 (Hijmans 2023). This distance was selected based on the average distance of

~1600 km between our *Glyptotherium* occurrence localities before spatial filtering, excluding the occurrences in Brazil, calculated using the geodesic distance function *distm* in the R 'geosphere' package ver. 1.5.18 (Hijmans 2022). This buffer corresponded to approximately 1000 grid cells from which the background points could be selected. The Antilles were removed from the buffer due to the paucity of fossils in that region (MacPhee 2005).

Niche modeling was performed in R ver. 4.2.2 (www.r-project.org) using the 'kuenm' package ver. 1.1.9 (Cobos et al. 2019). This package automates model calibration and selection by testing all combinations of feature classes, regularization multipliers, and environmental variables (Cobos et al. 2019). We produced 9548 candidate models using all combinations of feature classes (l = linear, q = quadratic, p = product, t = threshold and h = hinge), the four environmental variables (with a minimum of two variables per model), and regularization multipliers from 0.1 to 1.0 with intervals of 0.1, and from 2.0 to 5.0, with intervals of 1.0. Candidate models were evaluated using the 24 fossil localities with five-fold cross-validation and 1000 background points. Fewer background points were used than the default (10,000), since our buffer area only included a total of 1262 climatic grid cells, given the resolution of the paleoclimate data. Following Owens et al. (2013), we allowed for free extrapolation, which permits the model to extrapolate to conditions not encountered during calibration, but disallowed clamping, which 'clamps' the edge to the calibration region value. We tested whether extrapolation impacted inferred patterns by performing a multivariate environmental similarity surface (MESS; Elith et al. 2010) analysis, which examines the similarity between the climatic conditions at the training locations and the projection locations. The results of this analysis, which suggested none of the independent fossil localities are in regions of extrapolation, are reported in the Supporting information.

Models were selected in 'kuenm' based on the partial receiver operating characteristic analysis (partial ROC; Peterson et al. 2008), omission rates (E = 5, Anderson et al. 2003), and ΔAICc (up to 2, Burnham and Anderson 2002), which resulted in five best models. The five best models were then projected to the Middle (~2.194 Ma), Late Blancan (~3.094 Ma), and Blancan-Hemphillian (~4.47 Ma). The final five best models were further evaluated using area under the curve (AUC) of the partial ROC (Peterson et al. 2008), the continuous Boyce index (CBI; Boyce et al. 2002, Hirzel et al. 2006), the true skill statistic (TSS; Allouche et al. 2006), and kappa (Cohen 1960). All five models selected by 'kuenm' met our additional criteria of AUC > 0.70 and TSS > 0.4 (Zhang et al. 2015) (Table 1).

For each of the five best models, we calculated the median of the five cross-validation runs, and then took the median of the five median models, hereafter referred to as the double median model, using the *calc* function in the 'raster' R package ver. 3.6.14 (Hijmans 2023). We converted both the median models and double median model into binary suitability maps where 1 = suitable conditions and 0 = unsuitable conditions, based on two threshold metrics: maximizing the sum of sensitivity and specificity (maxSSS, Manel et al. 2001) and 98% least training presence (LTP, Pearson et al. 2007). The LTP threshold excludes 2% of occurrence points with the lowest suitability score and uses the threshold based on the remaining 98% of occurrences (Pearson et al. 2007). The maxSSS threshold takes the threshold that maximizes the sum of sensitivity and specificity (Manel et al. 2001). To calculate the threshold for the maxSSS double median models, we used the median of the median maximum training sensitivity plus specificity Cloglog threshold values output from Maxent.

Using these binary suitability maps, we calculated the consensus of the median models, hereafter referred to as the consensus model, using the *calc* function in the 'raster' R package ver. 3.6.14 (Hijmans 2023). For the Rancholabrean, the time interval in which the ENM was calibrated, we used this consensus model and tested whether three independent occurrences from Brazil, which were not used for training or testing, were predicted as corresponding to suitable conditions. Then, we projected the ENM into the other time intervals, again using the consensus models. We used the occurrences in each of those intervals to evaluate the model: Late Blancan (n = 6), Middle Blancan (n = 10), and Blancan-Hemphillian (n = 0). We assessed whether the occurrences intersected with suitable conditions more than expected by chance using binomial probabilities based on Saupe et al. (2019). We calculated the probability that the independent occurrences would overlap with suitable regions more than

Table 1. Results of median AUC (across five cross-validation runs), TSS, Kappa, and CBI for each of the five best models selected by 'kuenm' (Cobos et al. 2019). All models were run with extrapolation but without clamping.

Model	Regularization multiplier	Feature classes used	Median AUC (across five cross-validation runs)	TSS Value (for one cross-validation run)	Kappa (for one cross-validation run)	Continuous Boyce index value for training data
1	0.8	product, linear, threshold	0.77	0.64	0.14	0.88
2	0.8	product, linear, threshold, quadratic	0.77	0.62	0.15	0.91
3	0.8	product, threshold	0.77	0.64	0.14	0.87
4	0.8	product, threshold, quadratic	0.77	0.64	0.14	0.86
5	0.8	threshold	0.77	0.64	0.14	0.83

expected by chance for each time interval using the *dbinom* function in R, where *x* was the number of independent localities predicted, size was the number of independent localities, and the probability of a 'success' (i.e. an occurrence landing on suitable area) was the number of cells with suitable conditions divided by the number of cells in our study region. We considered statistical significance for the binomial test at an $\alpha = 0.05$. An overview of our methods workflow is presented in the Supporting information.

To test which migration corridors *Glyptotherium* or its ancestors may have utilized on their northward journey, we used circuit theory and least cost path analysis. Circuit theory is based on electrical circuit theory and uses the equivalent of resistance and current to model landscape connectivity (McRae et al. 2008). Least cost path analysis is a cost–distance metric that calculates the shortest cumulative cost-weighted distance between a given start and end point (Adriaensen et al. 2003). Both methods require an input in the form of a landscape resistance map. As in Bond et al. (2017), we created a landscape resistance map by taking the inverse of our ENM outputs (suitable conditions) and scaled them from 1 to 1000. For circuit theory we utilized the program 'Circuitscape' (ver. 4.0.5, McRae et al. 2016) via R (Marrotte 2015), and for the least cost analysis we used the function *costDistance* in the package 'gdistance' in R (van Etten 2017). We exclusively examined *Glyptotherium* in South America during the Blancan-Hemphillian, as this is the time and place we hypothesize that they or their ancestors would have used these corridors. Therefore, we cannot evaluate the Antilles route as it is not included in the climate model for the Blancan-Hemphillian. For the start and end points, we selected a point near the Panamanian Isthmus (7°N, 77°W) and one near the southern tip of South America (47°S, 70°30′W) to capture the full extent of the continent. Although these methods have been applied to corridors in the Pleistocene (Beyin et al. 2019, Ledo et al. 2020), few studies have been able to utilize the fossil record to assess corridors (Angulo et al. 2017). The resistance migration corridor analysis uses the suitability derived from a time averaged fossil record and estimated climate model. However, microclimates and extreme climatic conditions and fluctuations may influence the viability of a dispersal corridor, either positively or negatively. Therefore, our models provide a broad-scale overview of potential routes given the coarse spatial and temporal resolution of available data. All code can be accessed at https://doi.org/10.5281/zenodo.14429043.

Results

The five best models selected by 'kuenm' all include three of the four climatic predictors: minimum temperature of the coldest month, precipitation of the wettest month, and precipitation of the driest month, alongside varying regularization and feature classes (Table 1). These models had mean AUC values that ranged from 0.771 to 0.782, TSS values from 0.625 to 0.644, Kappa values from 0.135 to 0.145, and CBI values from 0.827 to 0.909 (Table 1). Our AUC and TSS values indicate a moderate model, although our Kappa values are poor (Zhang et al. 2015). CBI values suggest the model has good transferability to different regions. Overall, our model performs moderately. Across all models, the minimum temperature of the coldest month had the greatest contribution to model suitability (Supporting information).

MaxSSS threshold models predicted from 20% (Late Blancan; $n=1/5$) to 33.3% (Rancholabrean; $n=1/3$) of independent testing localities across time periods, whereas LTP threshold models predicted from 60% (Late Blancan; $n=3/5$) to 100% (Rancholabrean; $n=3/3$) of independent testing localities (Table 2, Fig. 2). The Middle Blancan LTP threshold models and the Rancholabrean double median LTP model performed significantly better than random at predicting the independent fossil occurrences based on binomial tests ($p < 0.05$). The maxSSS models were not significantly better than random at predicting the fossil occurrences (Supporting information).

For the consensus models, the area of the Americas predicted to be suitable for *Glyptotherium* in the Rancholabrean is 7.77% (maxSSS) to 16.0% (LTP). This number changes to 11.1% (maxSSS) and 29.0% (LTP) in the Late Blancan, to 12.2% (maxSSS) and 29.2% (LTP) in the Middle Blancan, and to 10.2% (maxSSS) and 28.1% (LTP) in the Blancan-Hemphillian.

All LTP suitability models (both consensus and double median) show continuous suitable conditions stretching from South to North America, with the exception of a small unsuitable area (possibly due to resolution dependency) around the Isthmus during the Rancholabrean and in the consensus model for the Late Blancan (Fig. 2). The maxSSS models (both consensus and double median) are less well connected in terms of suitable conditions, but do have suitable regions concentrated in Central America and the surrounding area (Fig. 2). The Rancholabrean is the only time interval for which there are paleoclimatic reconstructions for

Table 2. Independent test localities in each time interval and whether they correspond to projected suitable conditions.

Model	Total number of independent test fossil localities	Number of independent fossil localities predicted as suitable by LTP	Number of independent fossil localities predicted as suitable by maxSSS
Rancholabrean consensus	3	2 (66.7%)	1 (33.3%)
Rancholabrean double median	3	3 (100%)	1 (33.3%)
Late Blancan consensus	5	3 (60%)	1 (20%)
Late Blancan double median	5	3 (60%)	1 (20%)
Middle Blancan consensus	7	6 (85.7%)	2 (28.6%)
Middle Blancan double median	7	6 (85.7%)	2 (28.6%)

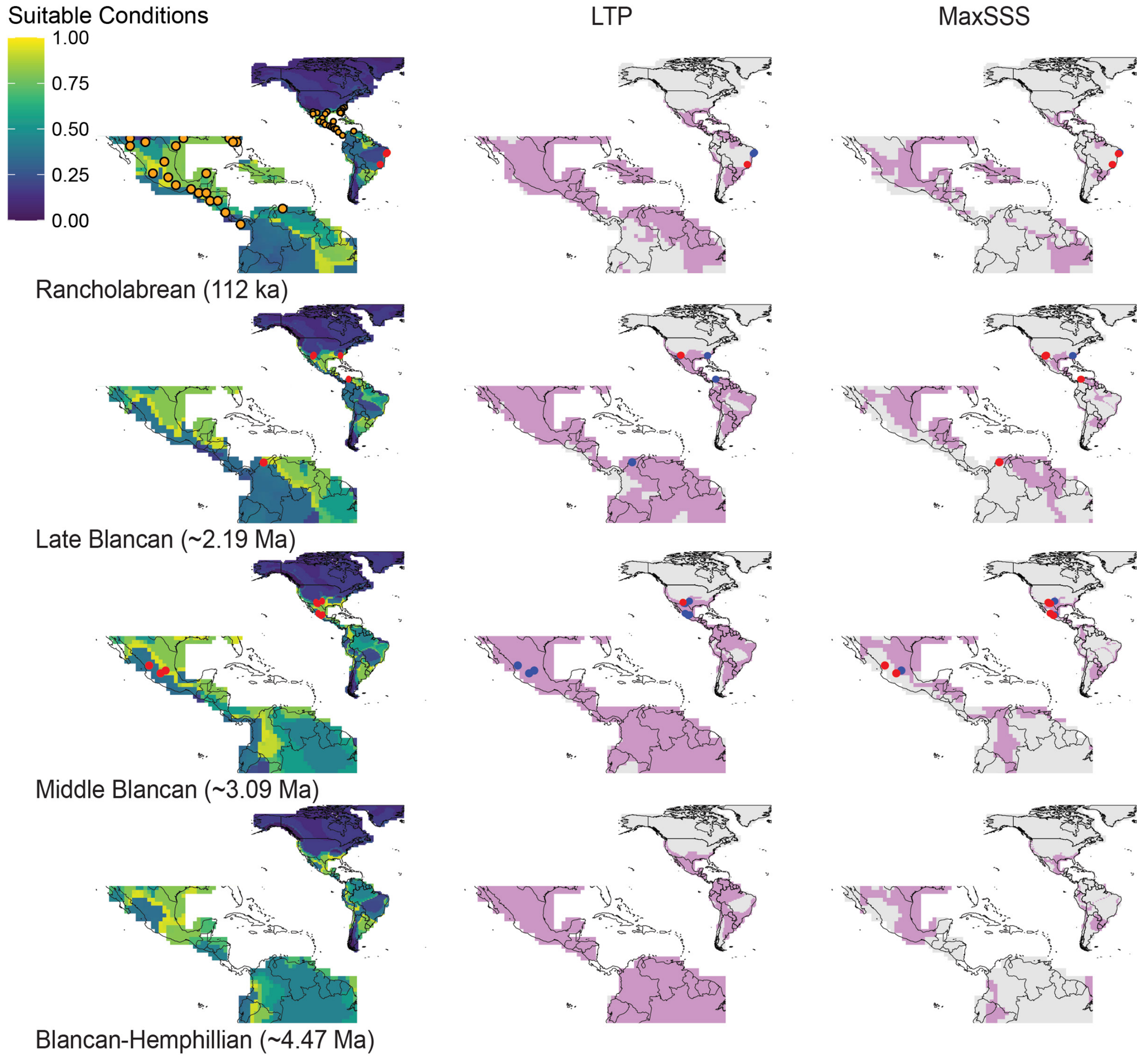

Figure 2. Median suitable conditions for *Glyptotherium* calibrated in the Rancholabrean using 24 spatially unique occurrences, projected to the Late and Middle Blancan and Blancan-Hemphillian. The LTP and maxSSS maps are examples of more and less conservative threshold estimates for suitable conditions, respectively. The orange points represent spatially filtered *Glyptotherium* localities for the Rancholabrean and the red and blue points are the independent testing localities for the projections. Consensus models for the Rancholabrean: 0.112 Ma, Late Blancan: ~2.19 Ma, Middle Blancan: ~3.09 Ma, and Blancan-Hemphillian: ~4.47 Ma. Light purple indicates suitable conditions and gray indicates non-suitable conditions for *Glyptotherium*. LTP and MaxSSS points in blue lie in places predicted to have suitable environmental conditions, whereas points in red are not (note that many of the occurrences overlap spatially at this scale for the Late and Middle Blancan intervals).

the Antilles, and all models indicate most or all of the Antilles as suitable for *Glyptotherium* (Fig. 2).

To make inferences about the ecological preferences of *Glyptotherium*, we extracted the maximum and minimum values for each of the environmental variables within the thresholded suitable conditions. The consensus area for *Glyptotherium* in the Rancholabrean had a range from 6.09 to 27.48°C (maxSSS) and 5.40 to 28.23°C (LTP) for the minimum temperature of the coldest month. Precipitation of the driest month ranged from 0.003 to 2.47 mm day^{-1} (maxSSS and LTP), whereas precipitation of the wettest month ranged from 1.31 to 6.36 mm day^{-1} (maxSSS) and 0.88 to 13.06 mm day^{-1} (LTP).

The circuit theory model predicts higher connectivity values along the eastern side of South America along the Andes and the 'high road,' whereas the least-cost path veers into

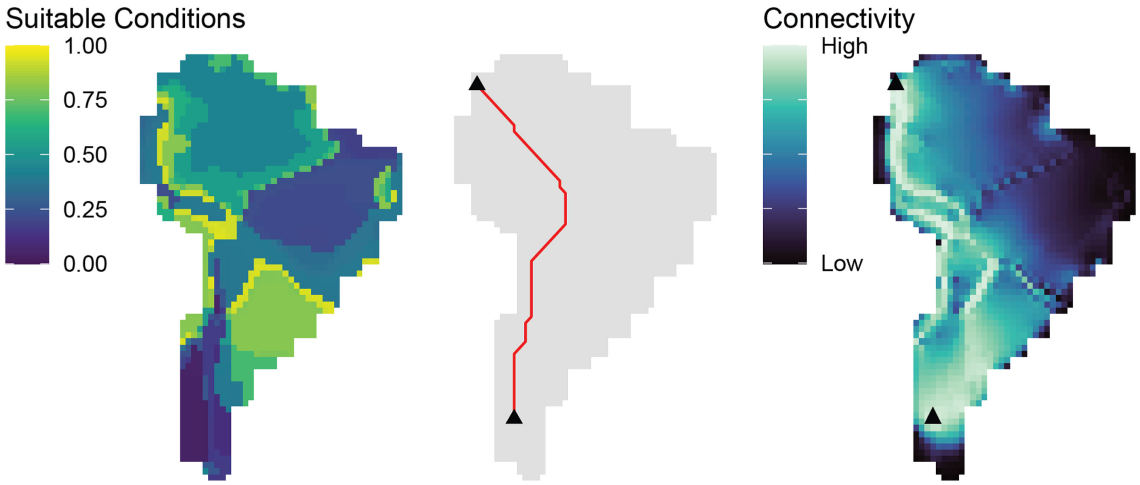

Figure 3. Results of the movement corridor analysis for South America during the Blancan-Hemphillian (~4.47 Ma). From left to right: raster map of ENM results for suitable conditions; red line showing least-cost path model; raster map of connectivity values from the circuit theory model (the color scale is histogram-equalized). Black triangles represent the start and end points for the models.

some of the more lowland areas in the northwest past of the continent (Fig. 3). The difference between the two paths is likely because the least-cost model assumes that animals have complete knowledge of the landscape, whereas circuit theory assumes their knowledge does not extend beyond their surroundings (i.e. adjacent cells) (McClure et al. 2016). Neither method predicts a path or high connectivity in the lowland Amazon on the northeast part of the continent (the 'low road').

Discussion

We evaluated suitable conditions for the genus *Glyptotherium* over the past five million years, which encompasses the GABI, using ecological niche modeling. We found that niche models predict relatively continuous suitable conditions for *Glyptotherium* throughout Central America and the surrounding region. This pattern supports previous hypotheses regarding *Glyptotherium* migration based on fossil localities. Analysis of movement corridors indicates that ancestors of *Glyptotherium* likely utilized the 'high road' in and around the Andes towards the western side of South America to reach central America. Our results also suggest it is also possible that *Glyptotherium* traveled through the Antilles, given the presence of suitable conditions in the region, at least during the Rancholabrean, the only time interval where we could assess this region.

Although our LTP models show that suitable conditions for *Glyptotherium* are present to migrate back to South America in the Rancholabrean, our maxSSS threshold models for the Rancholabrean give some pause to the idea that *Glyptotherium* may have migrated back to Northeastern Brazil during this time, as postulated by Carlini et al. (2008). This is because the Rancholabrean is the time interval with the fewest suitable regions in the 'low road', the most direct route to this location. We also identified two Irvingtonian (0.240–1.806 Ma) fossil localities in northeastern Brazil (Fig. 1), which may indicate that members of the genus stayed in South America throughout the Interchange.

Although our models provide insight into migration hypotheses, there are many sources of bias. The coarse spatial resolution of our climate model makes it difficult to discern finer scale suitability corridors. The fluctuating climate between the glacials and interglacials may have led to suitable corridors that were either too narrow or too brief for us to detect. Additionally, the relatively small number of well-dated fossil localities for *Glyptotherium* may have led to biased or truncated niche estimates, which will affect our understanding of geographic patterns of suitability. The lack of fossil localities also led us to model the niche at the genus level, which may obscure differences in the niches of individual *Glyptotherium* species. Furthermore, the projection of the niche model calibrated in the Rancholabrean to other time intervals (Middle and Late Blancan) assumes niche conservatism, which may not have been the case for *Glyptotherium*, especially at the genus level. Further work is necessary to examine whether *Glyptotherium* returned to South America in the Rancholabrean or simply remained in South America throughout the time interval of the Interchange.

Based on sedimentology, osteology, and community assemblages, Gillette and Ray (1981, p. 210) hypothesized that *Glyptotherium* would have needed 'warm climate without excessive extremes of temperature; and high, relatively constant moisture.' Our results support this hypothesis and suggest that *Glyptotherium* thrived under coldest month temperatures that were relatively warm and high levels of precipitation, with cold conditions potentially limiting its distribution.

Our ENM results suggest that *Glyptotherium* and the lowland species of its close relative, *Glyptodon*, may have had similar ecological requirements. *Glyptodon* appeared more recently in the fossil record than *Glyptotherium*, was slightly larger, and had different skull, dorsal carapace and caudal osteoderm morphology (Zurita et al. 2018). *Glyptodon* originated in South America and its earliest fossil record is from Argentina 1.07 Ma (Soibelzon et al. 2006, Zurita et al. 2018), over two million years after the oldest known *Glyptotherium*. Unlike *Glyptotherium*, the distribution of *Glyptodon* is restricted to South America (Zurita et al. 2018). *Glyptodon* consists of three species: *Glyptodon munizi* and *Glyptodon reticulatus*, which lived in the lowlands, and *Glyptodon jatunkhirkhi*, which lived in the higher elevation Cordillera (Cuadrelli et al. 2020). Of the lowland species, *Glyptodon munizi* appears first in the early Pleistocene and lasts until the middle Pleistocene, whereas *Glyptodon reticulatus* appears in the late Pleistocene and goes extinct in the early Holocene (Cuadrelli et al. 2018). Oliveira et al. (2010) reassigned Brazilian material from *Glyptodon* and *Chlamydotherium* to *Glyptotherium* (some of this material is now represented by our three Brazilian localities). The lowland species of *Glyptodon* have been categorized as selective feeders in closed environments based on morphological evidence (Vizcaíno et al. 2011), and isotopic evidence indicates they were flexible feeders (Domingo et al. 2012, Varela et al. 2023). Although *Glyptotherium* was likely a browser and *Glyptodon* may have been a more flexible feeder, there are also many similarities between the mandibles of *Glyptotherium* and *Glyptodon munizi* and *Glyptodon reticulatus* (Zurita et al. 2018).

Our models predict the area in southern South America where we find *Glyptodon munizi* and *Glyptodon reticulatus* fossils to be suitable for *Glyptotherium* (Fig. 2). Likewise, Varela et al. (2018) found that *Glyptodon munizi* and *Glyptodon reticulatus* had suitable conditions in the same areas of Northeastern Brazil that were also inhabited by *Glyptotherium* at that time based on their niche models of the Last Interglacial (LIG; equivalent to the Rancholabrean in our analysis). However, the inferred overlap has been established at coarse spatial scale, so it is possible that *Glyptodon* and *Glyptotherium* did not utilize the same habitat, with their geographic distributions being controlled by an environmental variable or interaction not included in our model. Additional analyses are needed to interrogate these patterns in more detail.

Further work across many taxa is needed to determine the existence of a Central American Filter and whether savanna expansion played a role in the Interchange. Work using track analysis has suggested that mammal species do not necessarily follow savannas in South America during the Pleistocene (Gallo et al. 2013). However, climate does appear to be important in range contractions and subsequent extinctions of South American mammals, which are correlated with the change from cold and dry to warm and wet conditions (Araújo et al. 2021). Our *Glyptotherium* results are also consistent with recent results that suggest colder climates were correlated with species dispersal during GABI (Freitas-Oliveira et al. 2024).

Conclusions

Our analysis indicates the presence of dispersal pathways with suitable conditions consistent with previously-hypothesized migration routes for *Glyptotherium*. Based on our niche models, *Glyptotherium* likely had a corridor of suitable conditions to North America via the 'high road' in the northwest of South America during the Plio-Pleistocene and possibly back to South America during the Rancholabrean. Patterns of environmental suitability suggest members of the genus may have traveled along the east coast of South America or through the Caribbean via the Antilles. However, further work is necessary to determine if the 'Central American filter' (Simpson 1950) is climatic in nature or if there are other factors at play for *Glyptotherium,* or in fact for any other taxon. Our results also indicate that *Glyptotherium* and the lowland species of *Glyptodon* may have a similar climatic niche. Based on our model and the distribution of fossil localities, it appears the two taxa had similar ecological needs, at least with regard to the environmental variables we modeled.

Acknowledgements – We would like to thank Gary Morgan and Ascanio Rincón for knowledge and advice on Glyptodonts. Thanks also to Miranta Kouvari at Science Graphic Design for her design assistance for Fig. 1. Jack Tseng provided helpful comments on an earlier version of the manuscript.

Funding – KMM was funded by the Berkeley Chapter of Sigma Xi, Phi Beta Kappa of Northern California, the University of California Museum of Paleontology, and the Department of Integrative Biology at University of California, Berkeley. EES was supported by a Leverhulme Prize and NERC grant no. NE/V011405/1. AF acknowledges the Natural Environment Research Council of the UK (grant no. NE/X015505/1, NE/V011405/1 and NE/X018253/1) and the Chinese Academy of Sciences Visiting Professorship for Senior International Scientists (2021FSE0001). CRM was partially supported by the Philip Sandford Boone Chair in Paleontology.

Author contributions

Katherine M. Magoulick: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Methodology (supporting); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **Erin E. Saupe**: Conceptualization (supporting); Formal analysis (equal); Methodology (lead); Supervision (equal); Writing – original draft (equal); Writing – review and editing (equal). **Alexander Farnsworth**: Simulations (equal); Resources (equal); Writing – review and editing (supporting). **Paul J. Valdes**: Resources (equal). **Charles R. Marshall**: Conceptualization (supporting); Project administration (equal); Supervision (equal); Writing – original draft (equal); Writing – review and editing (equal).

Transparent peer review

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ecog.07499.

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.ghx3ffc08 (Magoulick et al. 2024). Code is available at: https://doi.org/10.5281/zenodo.14429043

Supporting information

The Supporting information associated with this article is available with the online version.

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