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**Facultad de Ciencias Naturales y Oceanográficas**

**Magíster en Ciencias con mención en Zoología**

**UNTANGLING THE CAUSES OF TERROR BIRDS EXTINCTION  
(CARIAMIFORMES, PHORUSRHACIDAE): THE INTERPLAY OF BIOTIC  
AND ABIOTIC FACTORS**

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## **STATEMENTS**

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## RESUMEN

Los patrones de biodiversidad a lo largo del tiempo están determinados por una compleja interacción de factores bióticos y abióticos. Los Phorusrhacidae (aves del terror), depredadores ápice de Sudamérica durante gran parte del Cenozoico, se enfrentaron a la extinción a través de mecanismos que siguen siendo poco conocidos. En este trabajo, utilizando datos de ocurrencia de fósiles y modelos bayesianos de diversificación, comprobamos cómo los cambios ambientales y las interacciones bióticas influyeron en su dinámica evolutiva. Encontramos que las tasas de especiación se correlacionan positivamente con la autodiversidad, los niveles atmosféricos de CO<sub>2</sub> y la diversidad de Sparassodonta, mientras que las tasas de extinción aumentan con la diversidad del propio linaje, la apertura del hábitat y la diversidad de Carnivora y Didelphimorphia. Nuestros resultados apoyan un modelo mixto Reina Roja-Bufón de la Corte, en el que tanto la competencia biótica como los grandes cambios ambientales contribuyeron sinérgicamente a la extinción de Phorusrhacidae. Esto subraya la necesidad de tener en cuenta causas multifactoriales a la hora de reconstruir las trayectorias evolutivas de los clados dominantes.

**Palabras clave:** Phorusrhacidae, biodiversidad del Cenozoico, Hipótesis de la Reina Roja, Hipótesis del Bufón de la Corte, dinámica de extinción, Sudamérica.

## ABSTRACT

Biodiversity patterns through time are shaped by a complex interplay of biotic and abiotic factors. The Phorusrhacidae (terror birds), apex predators of South America during much of the Cenozoic, faced extinction through mechanisms that remain poorly understood. Here, using fossil occurrence data and Bayesian diversification models, we test how environmental changes and biotic interactions influenced their diversification dynamics. We find that speciation rates positively correlate with self-diversity, atmospheric CO<sub>2</sub> levels, and Sparassodonta diversity, while extinction rates increase with self-diversity, evolution of open habitats and the diversity of Carnivora and Didelphimorphia. Our results support a mixed biotic-abiotic model, where both biotic competition and major environmental shifts contributed synergistically to the extinction of Phorusrhacidae. This emphasizes the need to consider multifactorial causes when reconstructing the evolutionary trajectories of dominant clades.

**Key Words:** Phorusrhacidae, Cenozoic biodiversity, Red Queen Hypothesis, Court Jester Hypothesis, Extinction dynamics, South America.

## INTRODUCTION

Biodiversity arises from a complex interaction of biotic and abiotic factors, which evolve over time and across different environments [1]. Biotic factors encompass the ecology and physiology of organisms, their interactions, and community structure, whereas abiotic factors involve geochemical cycles, geological processes, and changes in climate and landscape. These factors are highly relevant as they influence evolutionary rates and ultimately shape the evolution of biodiversity [2]. Consequently, two macroevolutionary models have been proposed to explain the generation and maintenance of diversity [3]. The Red Queen model [4, 5] posits that these dynamics are primarily driven by biotic factors intrinsic to species [6-8], while the Court Jester model [9] asserts that they result from historical abiotic forces [10, 11]. Scenarios that incorporate both models can occur, known as mixed models [3, 12, 13].

The family Phorusrhacidae, commonly known as '*terror birds*,' refers to a group of extinct land birds that were dominant predators during the Cenozoic in South America (Annex 1) [14-18]. They were characterized by generally large bodies (gigantism in the subfamilies Phorusrhacinae and Physornithinae), reinforced skulls, and in some cases, entirely akinetetic, long and strong hind limbs [19, 20], reduced forelimbs [15, 18, 21], curved and laterally compressed nail phalanges [18, 22], and a high, long, and laterally compressed hooked bill [21], which is absent in any other bird, either extinct or extant [19]. This unique feature supports its carnivorous diet [17]. Terror birds represent the most diverse clade within the Cariamiformes order, currently represented by only

two extant species [21]. Phorusrhacids comprise the subfamilies Psilopterinae, Mesembriornithinae, Patagornithinae, Phorusrhacinae, and Physornithinae [20]. Although primarily found in South America, with a fossil record dating from the Eocene to the Pleistocene (younger specimens in Uruguay, associated with the late Pleistocene [16]) [18, 19, 21], they were able to migrate to North America in the Pliocene during the Great American Biotic Interchange (GABI). Some remains found in Europe and Africa have been assigned to this clade. However, these assignments remain controversial [22-25].

To explain the evolutionary dynamics of Phorusrhacidae, factors related to both the Red Queen model and the Court Jester model (competition or environmental hypotheses [19]) have been suggested. However, despite recent advances, the drivers for their disappearance remain unclear [18, 21, 24, 26]. The Red Queen model suggests that terror birds went extinct primarily due to competition with North American placental carnivores [19, 27, 28]. However, the existence of species such as *Titanis walleri*, which successfully dispersed to North America during the GABI, indicates they were not among the early lineages affected by competition or predation during the interchange, even though their time in North America appears to have been ephemeral [24]. Consequently, it remains unclear whether terror birds were disadvantaged in direct competition with placental carnivores or if their diversity declined before the GABI, leading to their extinction [14, 26]. In this context, during much of the Cenozoic, the carnivore niche of South America was occupied by non-mammalian groups such as Phorusrhacidae, Sebecidae, and Madtsoiidae, along with the metatherian group, Sparassodonta, and from the late Miocene

to the mid-Pliocene also included didelphimorph marsupials [29]. Therefore, these groups could have been potential competitors [11]. Yet, the diversity of sebecid crocodiles and madtsoiid snakes was low during the Cenozoic, and their extinction preceded that of terror birds [29]. Phorusrhacidae and the large carnivorous Sparassodonta possibly competed for the same resources; among them, *Borhyaena*, one of the few cursorial sparassodonts, was probably their main competitor [19, 20]. Additionally, the evolution of body size in Phorusrhacidae is an intrinsic biological factor that may have influenced their diversity. This occurs because widespread selection for larger body sizes in carnivores often results in dietary specialization (hypercarnivory) and increased vulnerability to extinction, as evidenced by the extinction of Miocene-Pliocene North American canids [30]. Furthermore, the evolution and variation in body size drove niche partitioning among terror birds and competitive exclusion-driven phorusrhacids diversity [20].

Some studies suggest that the extinction of Phorusrhacidae may be linked to abiotic factors, which aligns with the Court Jester model. Thus, it has been proposed that geological and climatic changes could have constituted the primary drivers for the demise of terror birds, drawing parallels from the analogous patterns observed in other native South American groups [11, 31, 32]. Multiple environmental transformations in South America throughout the Cenozoic are directly or indirectly associated with the timing and intensity of the Andean orogeny and the decline in global temperatures. These changes, in turn, resulted in a transition from the predominantly warm, forested habitats of the early Cenozoic to a climate regime characterized by cooler, drier

conditions accompanied by seasonal aridity [27, 29]. Consequently, the biota is expected to exhibit appearances, extinctions, extirpations, or component alterations [19]. Considering this context, the biota of South America experienced major climatic, tectonic, and geographic changes during the Cenozoic, which notably affected its evolution and extinction [11, 31, 33]. This may have also influenced the diversification dynamics of the family Phorusrhacidae.

In this study, we analyzed the fossil record of the Phorusrhacidae family and others coexisting groups in South America to assess the potential impact of biotic and abiotic factors on their decline and eventual extinction using Bayesian diversification models. It involved inferring rates of origin and extinction over time for the Phorusrhacidae family and evaluating whether fluctuations in these rates can be linked to climatic and geological factors, biotic interactions with potential competing clades, and body mass evolution.

## METHODS

### Fossil occurrence datasets

We compiled fossil occurrence datasets at the species level for Phorusrhacidae and its putative competitors (Carnivora order and the carnivore species of the metatherian groups, Sparassodonta and Didelphimorphia). The Phorusrhacidae fossil occurrences were extracted from the Palaeobiology Database (PBDB; <https://paleobiodb.org/>; downloaded December 2024). The fossil datasets for the proposed competitor groups were obtained from a comprehensive dataset of all South American fossil mammals (Pino *et al.* unpublished data). This broader dataset was compiled from the PBDB, to which K. Pino contributed ~500 new entries, the New and Old Worlds database of fossil mammals ([www.nowdatabase.org/](http://www.nowdatabase.org/)), and published literature [11, 31]. The compiled datasets were cleaned using a pipeline to identify potential spatial, period, and taxonomy (synonyms, misspellings, and duplicates) errors with *CoordinateCleaner* and *Fossilbrush* R packages [34, 35]. The flagged occurrences were then inspected manually. The occurrence ages associated with the SALMAs (South American Mammals Ages) and some collections were updated with more recent dates [36-39]. We used the 'look\_up' function implemented in the *palaeoverse* R package [40]. We supplied the interval key argument with our updated ages—occurrences with a temporal range larger than 15 million years were excluded (Annexes 2; 3) [7]. The taxonomy of the phorusrhacids was revised and standardized based on the latest specialized literature (Annex 4). We excluded *Paleopsilopterus*

*itaboraiensis* and *Patagorhacos terrificus*, as their classification within Phorusrhacidae is debated and relies on very fragmentary evidence [20]. Because the oldest uncontroversial record of Phorusrhacidae, which dates from the middle Eocene of Argentina [22], and the most recent record, which dates from the late Pleistocene of Uruguay [16], correspond to indeterminate species of the subfamily Psilopterinae, the fossil occurrences of phorusrhacids considered in our analysis range from the Late Oligocene to the Late Pliocene (29.4 - 3.04 Ma; Figure S1). The final datasets include 16 species of Phorusrhacidae (70 occurrences), 66 species of Carnivora (382 occurrences), 68 species of Sparassodonta (161 occurrences), and 25 species of Didelphimorphia (80 occurrences). Finally, to account for dating uncertainties in the estimated rates, we resampled the age of each occurrence uniformly from its age range using the *'extract.ages'* R function from the R utility script included in the PyRate package. We generated 100 random datasets for each group and imported them into PyRate for diversification rate analysis [41, 42].

### **Diversification rates estimation**

Phorusrhacids origination and extinction rates and their putative competitors were estimated using the rate-shifting birth-death model (BDS) implemented in PyRate [41]. This program implements a Bayesian framework to analyze fossil occurrence data to estimate preservation, origination, and extinction rates while incorporating several sources of uncertainty [41]. PyRate includes three preservation models: the Homogeneous Poisson Process (HPP), the Non-Homogeneous Poisson Process (NHPP), and the Time-Varying Poisson Process (TPP). Therefore, a maximum likelihood test was performed to select

the preservation model that best fits the data. We used a gamma model to allow for rate heterogeneity through time (stages of the stratigraphic geological time scale) and across lineages coupled with the best-fitted preservation model. In conjunction, a Reversible Jump Markov Chain Monte Carlo (RJMC) algorithm was used to estimate the origination and extinction rates and their temporal variation. This algorithm explicitly estimates statistically significant rate changes number and temporal location and avoids sub- and over-parametrization [41]. We conducted 50 million iterations, sampling every 5000 for the Phorusrhacidae, Carnivora, and Didelphimorphia groups while performing 140 million iterations with sampling every 14000 for Sparassodonta to ensure convergence. After excluding the first 10% of the samples as burn-in, we combined posterior samples from the 100 randomized datasets and summarized the parameters by calculating their mean and 95% credible intervals. Finally, we used the origination and extinction times estimated by the BDS model for all sampled species to generate diversity trajectories across time for all groups (Figure S2).

### **Biotic and abiotic factors of diversification dynamics**

To assess how biotic and abiotic factors can explain temporal variation in origination and extinction rates, we used the multivariate birth-death model (MBD) implemented in PyRate [43]. Under this model, a single analysis can infer which and how many variables abiotic and biotic factors considered significantly explain the origination and extinction rate dynamics. At the same time, it calculates shrinkage weights ( $Wl$  for speciation and  $Wm$  for extinction) to quantify the statistical support for all predictors (factors), their signs, and

intensity. When these weights exceed 0.5, it indicates significant support for the corresponding correlation parameters ( $G_I$  for speciation and  $G_m$  for extinction) [43]. We employ the horseshoe prior algorithm to shrink the correlation parameters around zero, thus reducing the risk of over-parameterization and the need for explicit model testing [43].

A total of 11 variables were considered (4 biotic and 7 abiotic factors). In the case of biotic variables, diversity trajectories estimated with the BDS model for putative competitors (Carnivora order, Sparassodonta, and Didelphimorphia) were used under the assumption that biotic interactions can be measured as diversity-dependent rates of origin and extinction [7, 11]. The diversity of phorusrhacids was also considered, as their diversity may affect their diversification dynamics. For the abiotic variables, we considered the time-continuous Andean paleo-elevation as a proxy for regional environmental and landscape change [44]. We used the smoothed mean curve estimated for the entire Andes obtained from the individual geomorphological domains reconstructed by Boschman [45] (see Boschman and Condamine [46] for detailed methods). Since the fossil record of phorusrhacids is predominantly found in southern South America (SSA; Figures S3 – S5), local geological and environmental changes likely influenced their diversification dynamics more significantly than broader regional factors. Therefore, we considered the paleo-elevation data for the central-southern (CS) Andes (geomorphological domains 4 to 7, Fig. 1) [46], along with the leaf area index (LAI) [47] and proportion of open habitat as proxies of the expansion of the arid biomes (i.e., grasslands, savannas) in SSA over the Cenozoic [48]. Finally, we considered

the climatic global variables: mean temperature variation (sourced from [49]), mean sea-level reconstruction (obtained from the Tectono-Glacioeustatic curve developed by Van der Meer *et al.* [50]), and mean carbon dioxide levels (derived from [51]; CenCO2PIP; downloaded January 2024). These proxies of global environmental changes are hypothesized to be associated with changes in biodiversity at local and regional scales [31, 52]. To conduct the MBD analyses, the trajectories of biotic and abiotic variables were rescaled to range between 0 and 1 (Annex 2) . We ran 150 million MCMC iterations, sampling every 3000 to estimate the model parameters. To summarize the results of the MBD analyses, we calculated the posterior mean and 95% HPD (Highest Posterior Density) of all correlation parameters and the mean of the respective shrinkage weights through 99 converged replicates.

### **Diversification dynamics and their correlation with body mass evolution**

To test whether the diversification dynamics of phorusrhacids are correlated with body mass evolution (intrinsic biotic factor), we used the Covar birth-death model [42], implemented in PyRate. In the Covar model, the variation in speciation and extinction rates is correlated with a continuous trait, specifically (log-transformed) body mass [42], through the parameters  $\alpha_\lambda$  and  $\alpha_\mu$ . Thus, a correlation (positive or negative) exists between the trait and rate changes if the posterior estimate of the correlation parameters differs significantly from zero [7]. Birth-death rates are, therefore, transformed on a lineage-specific basis rather than through time. Thus,  $\alpha > 0$  indicates a positive correlation between the trait value and the birth-death rates,  $\alpha < 0$  shows a negative correlation, and  $\alpha \sim 0$  denotes no correlation. Data on body mass for

phorusrhacids species is limited; consequently, we used the width of tarsometatarsal trochlea III as a proxy for body mass, as it correlates linearly with femur length (FL) in phorusrhacids (Supplementary Material of LaBarge et al. [20]). Femur length is a reliable indicator of body mass in birds [20]. We ran 100 replicates, fixing the times of speciation and extinction to the ages estimated from 100 replicated data sets under the BDS model. We ran 50 million MCMC iterations with a sampling frequency of 5000 and combined the posterior samples of the parameters from the 100 replicates after excluding the first 1000 samples as burn-in.

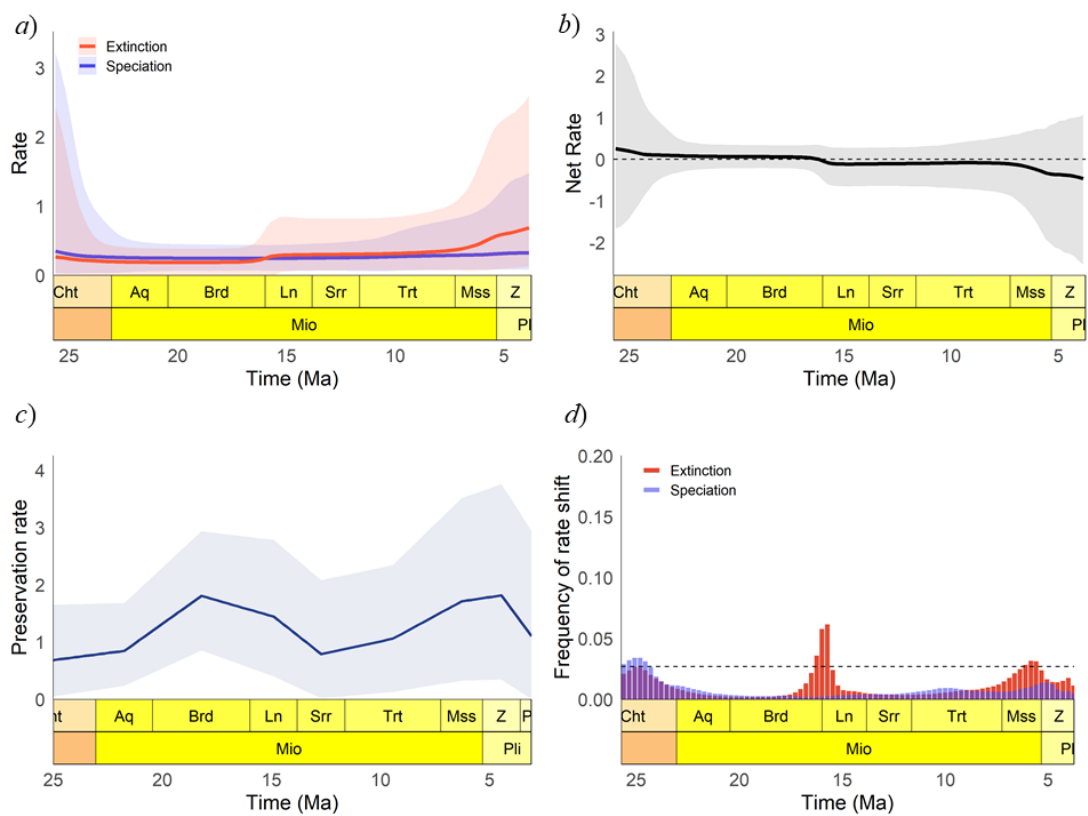
## RESULTS

### **Phorusrhacidae diversification dynamics**

Phorusrhacidae exhibits a diversification pattern characterized by a strong positive net diversification rate since the Late Oligocene, followed by a slight decrease around 24 Ma. This rate remained constant until the middle Miocene (~16 Ma), where a negative net diversification rate led the group to extinction (death age: 3.02 Ma; 95% HDP: 1.8913 - 3.7353) (Fig. 1*b*). This can be explained by two significant increases ( $\log BF > 2$ ) in extinction rate during the Miocene about 16 and 6 Ma ago until the disappearance of the clade (Figure 1*d*). Interestingly, the high extinction rate during the Late Miocene coincides with the extinction of the subfamilies Patagornithinae and Phorusrhacinae (Fig. S2). Moreover, the speciation rate remains constant over the studied time, with no significant increases or decreases (Figure 1*d*). Therefore, this indicates that the disappearance of phorusrhacids was caused by increases in the extinction rate during the middle and late Miocene.

The best-fitting preservation model for phorusrhacids was the time-variable Poisson process, indicating that preservation rates are heterogeneous across time bins (i.e., stages). The average preservation rate was 1.2378 (95% HDP: 0.7432-1.7743), with the highest preservation rates occurring during the Early Miocene (Burdigalian; mean 1.8063; 95% HDP: 0.8557-2.9346) and Late Miocene (Messinian; mean 1.7103; 95% HDP: 0.3270-3.5112) to Early Pliocene (Zanclean; mean 1.8163; 95% HDP: 0.3464-3.7562) and the lowest during the Late Oligocene (Chattian; mean 0.6636; 95% HDP 0.0279-1.6459)

(Fig. 1c). Whereas the best-fitting preservation models for the putative competitors were non-homogeneous Poisson process, homogeneous Poisson process, and time-variable Poisson Process for Sparassodonta, Didelphimorphia and Carnivora, respectively.



**Figure 1.** Diversification and preservation rates of Phorusrhacidae. (a) Rates of speciation and extinction. (b) Net diversification rate. The horizontal dashed line indicates net rate = 0. (c) Preservation rates over time are estimated using the time-varying Poisson model. Solid lines indicate mean rates, while shaded areas represent 95% credible intervals. (d) Frequencies of shifts in speciation and extinction rates, the horizontal dashed line indicates the threshold for positive (log BF = 2) evidence of a rate shift.

## **Phorusrhacidae diversification dynamics correlation with biotic and abiotic factors**

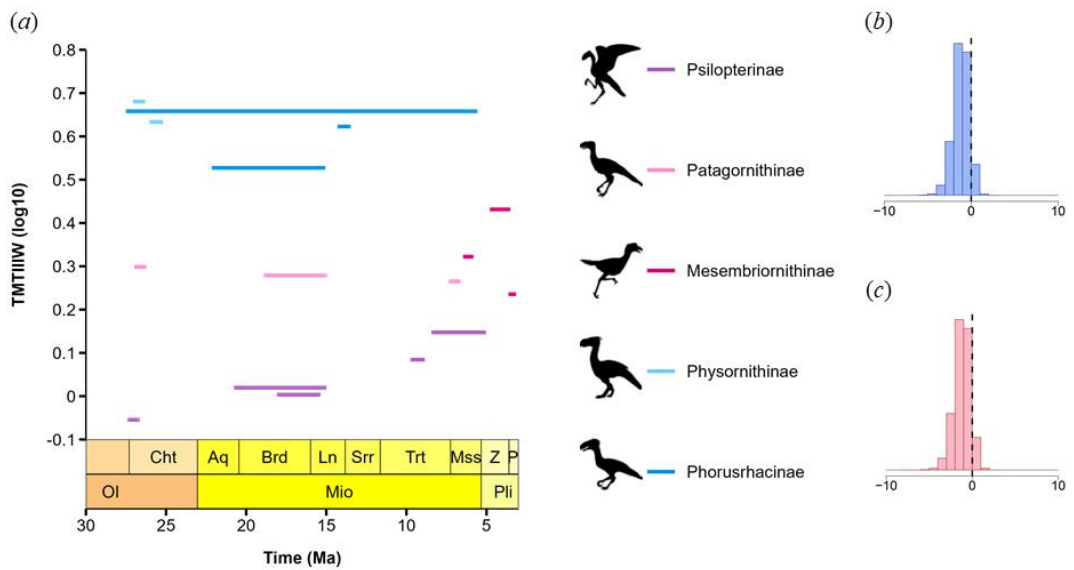
The MBD results show significant correlations between the diversification dynamics of phorusrhacids and biotic and abiotic factors. We find that speciation and extinction rates are diversity-dependent processes. The diversity changes of the potential competitors, Didelphimorphia and Carnivora, as well as the self-diversity of the group, show a significant positive correlation with the extinction rate of Phorusrhacidae (shrinkage weight  $w > 0.5$  and correlation parameters  $G_e = 0.451$ ;  $0.061$ ; and  $1.630$ , respectively) (Table 1). Additionally, the self-diversity of phorusrhacids is negatively correlated with the group's speciation rate ( $w = 0.918$ ,  $G_s = -3.372$ ). In contrast, the diversity trajectory of Sparassodonta shows a significant positive correlation with the speciation rate of phorusrhacids ( $w = 0.506$ ,  $G_s = 0.551$ ). Among the abiotic factors considered in our analysis, we found a significant positive correlation between the global carbon dioxide levels and speciation rate ( $w = 0.578$ ,  $G_s = 0.207$ ). Additionally, one of the proxies of the open habitats expansion in the SSA, the leaf area index, positively correlates with the extinction rate ( $w = 0.690$ ,  $G_s = 1.146$ ). Finally, none of the other variables included in this analysis were significantly correlated with Phorusrhacidae diversification rates (Table 1).

**Table 1.** Multiple birth-death model summary results of the phorusrhacids diversification dynamics correlation with biotic and abiotic factors. Shrinkage weights,  $w > 0.5$ , indicate significant support (in bold) for the corresponding correlation parameters ( $G_s$  for speciation and  $G_e$  for extinction).

Factors			Speciation		Extinction	
			$G_s$	$W_s$	$G_e$	$W_e$
Biotic		Self-diversity	<b>-3.372</b>	<b>0.918</b>	<b>1.630</b>	<b>0.806</b>
		Sparassodonta diversity	<b>0.551</b>	<b>0.506</b>	0.003	0.356
		Carnivora diversity	0.008	0.485	<b>0.061</b>	<b>0.501</b>
		Didelphimorphia diversity	0.280	0.440	<b>0.451</b>	<b>0.534</b>
Abiotic		Andean uplift (all domains)	0.041	0.459	-0.010	0.450
	Regional	Andean uplift (CS domains)	0.023	0.439	-0.020	0.475
	Local	Leaf area index	-0.030	0.268	<b>1.146</b>	<b>0.690</b>
		Open habitat proportion	0.091	0.302	-0.011	0.303
		CO <sub>2</sub> level	<b>0.207</b>	<b>0.578</b>	0.069	0.499
	Global	Temperature	0.068	0.422	-0.004	0.419
	Sea level	0.125	0.361	-0.038	0.360	

### Phorusrhacidae diversification dynamics correlation with body mass evolution

The estimated correlation parameters ( $\alpha_\lambda$  and  $\alpha_\mu$ ) were not significantly different from zero (Fig. 2). Therefore, we find no evidence of a correlation between the evolution of body mass and the estimated dynamics in speciation and extinction rates.



**Figure 2.** Correlation between phorusrhacids diversification dynamics and its body size evolution. (a) Phorusrhacids body mass over time. Tarsometatarsus trochlea III width (TMTIIIW). Lines represent the estimated life span of each species obtained from BDS analyses. Colors denote the main phorusrhacid subfamilies. Posterior frequencies of the estimated correlation parameters between body mass and speciation (b) and extinction (c) rates. Silhouettes (*Psilopterus lemoinei*, *Patagornis marshi*, *Paraphysornis brasiliensis* and *Phorusrhacos longissimus*, by Thomas W. LaBarge: CC BY 4.0; *Llallawavis scagliai* by Zimices (Julián Bayona): CC BY-NC 3.0) sourced from PhyloPic.

## DISCUSSION

The diversification history of Phorusrhacidae is characterized by a constant net diversification rate throughout most of the Oligocene and early Miocene. However, increases in the extinction rate during the middle (~16 Ma) and late Miocene (~6 Ma) resulted in the demise and eventual extinction of the group. Interestingly, the highest preservation rates are during these same time-bins (see results, Fig. 1), providing strong empirical evidence for the biological signal of the estimated shifts in extinction rates. The fossil record is inherently incomplete and biased [31]. Nonetheless, we employed a cutting-edge Bayesian framework to estimate speciation and extinction rates while accounting for the preservation process (including fossilization, sampling, and taxonomic identification biases) and uncertainties related to the age of fossil occurrences. Simulated and empirical datasets with limited fossil occurrences have shown the accuracy and robustness of these models [32, 41, 42, 53].

Furthermore, we found evidence of diversity-dependent biotic interactions, the negative effects of the evolution of open areas, and subsequent landscape changes on the continent affecting phorusrhacids' speciation and extinction rates. Consequently, this suggests that the interplay of biotic and abiotic factors influenced the diversification dynamics of Phorusrhacidae and ultimately contributed to their extinction in the Late Pleistocene, according to the dating of most recent records assigned to indeterminate species of the subfamily Psilopterinae [16].

## Red Queen model

Evolutionary rates in Phorusrhacidae are significantly correlated with diversity dependence (negatively with speciation rate and positively with extinction rate; Table 1). This may be a product of ecological constraints caused by competition for resources or by limited availability of ecological niches [66, 67]. Potentially, interactions with other groups (or different branches of the same lineage), limits on environmental productivity, the species' abundance, and the extent of habitable space or suitable environmental conditions are potential mechanisms that can generate diversity dependence trajectories [32, 72]. Thus, the effects of diversity on diversification dynamics would act through speciation when the emergence of new taxa is hampered by a lack of ecological opportunities in crowded habitats or through extinction, resulting from competitive displacement by ecologically similar taxa [68]. In this context, what appears to be a unique case of intraguild competition between members of Patagornithinae and Mesembriornithinae (composed of pursuit mesopredators) has been proposed since both subfamilies seem to have occupied the same niche in the same habitat and. Consequently, the competition ultimately led to the extinction of Patagornithinae. During the Huayquerian, the emergence of *Mesembriornis incertus*, a niche competitor akin to *Andalgalornis steulleti*, closely precedes the extinction of Patagornithinae as the transition to the Montehermosan SALMA occurs [20]. Similarly, several studies carried out in other groups have also shown a negative relationship between species diversity and speciation rates (e.g., 31, 32, 67, 69-74), as well as a negative or positive correlation between extinction

rate and species diversity (e.g., 68, 75, 76). Thus, global regulation of diversity through negative diversity dependence appears to be a common feature of nature.

Our results provide evidence that competition contributed to the extinction of terror birds, as changes in the extinction rates of phorusrhacids are correlated with diversity changes of competitors Carnivora and Didelphimorphia. Procyonids of the '*Cyonasua group*' were the first placental carnivores to arrive from North to South America during the late Miocene, before the complete emergence of the Isthmus of Panama [54]. The group comprising the extinct genera *Cyonasua* and *Chapalmalania* are the only placental carnivores in South America with a fossil record extending nearly 4.3 Ma [11, 55]. Members of the *Cyonasua* group exhibited greater specialization for carnivory than most extant procyonids [55, 56], with body masses ranging from 3 to 24 kg for *Cyonasua* and around 25 to 93 kg for *Chapalmalania* [57] (some estimates suggest a mass between 93 to 154 kg for *Chapalmalania* [57]). Thus, members of the *Cyonasua* group were likely to compete for similar prey with members of the subfamily Psilopterinae, which includes small species (e.g., *Procariama simplex* 9.48-12.66 kg [18]), as well as species from Mesembriornithinae (e.g., *Mesembriornis milneedwardsi* 53.84-66 kg [18], 70 kg [24]) composed by medium-sized species [20]. Furthermore, morphofunctional studies of Pliocene didelphimorphs indicate a significant increase in body size and carnivorous habits compared to pre-Pliocene lineages, notably more specialized than their present-day relatives [56]. Hence, several distinct carnivorous morphotypes evolved during the late Miocene to Pleistocene,

distributed in two main groups: Sparassocynidae and Didelphidae [29]. Specifically, members of Sparassocynidae, including *Thylorhynchops*, *Thylatheridium*, and *Hyperdidelphys*, evolved into highly carnivorous taxa [58]. Terror birds exhibit a temporal overlap with didelphimorphs and were contemporary during the evolution of their highly carnivorous forms. Thus, it is likely that these carnivorous didelphimorph taxa compete with certain species of Phorusrhacidae.

In contrast, changes in Sparassodonta diversity positively affect the phorusrhacids' speciation rate, rejecting the competition hypothesis between these groups. This result could be interpreted as potential positive interactions between these two carnivorous groups or similar responses to a common factor driving their diversification dynamics. Beneficial interactions between Sparassodonta and terror birds have been proposed in previous studies [59, 60]. Most sparassodonts were hypercarnivorous, although some displayed omnivorous or insectivorous diets [61]. Among them, *Thylacosmilus atrox*, a highly specialized saber-toothed predator, evolved extreme adaptations such as hypertrophied upper canines and was the last large Sparassodonta (~120 kg) during the late Miocene to Pliocene [29, 31, 62]. As a top carnivore, it probably left large prey partly uneaten because it could not process bones, which attracted scavengers like terror birds and small metatherians [59, 60]. It has also been suggested that some borhyaenids may have hunted prey while phorusrhacids scavenged the remains [59]. Therefore, some Sparassodonta taxa may have benefited certain phorusrhacids. Furthermore, it has been proposed that terror birds replaced the large carnivorous borhyaenids of the

subfamily Borhyaeninae in the late Tertiary, at least in the savannas of Argentina [63]. On the other hand, Phorusrhacidae exhibit spatial and temporal overlap with Sparassodonta, and their diversity trajectories appear to follow a similar trend, suggesting a common cause driving the decline of both clades [11, 31, Fig. S2, this study]. Yet, previous studies on the potential drivers of Sparassodonta diversification dynamics point to the drastic geological, environmental, and climatic changes triggered by the uplift of the Andes as the primary cause of its demise [11, 31, 64]. Thus, our results contribute to previous studies that dismiss the competition hypothesis between sparassodonts and terror birds [11, 31, 65]. However, the explanation for the positive relationship between sparassodonts diversity and phorusrhacids diversification remains unresolved.

### **Court Jester model**

A significant and positive correlation can be observed between the speciation rate of Phorusrhacidae and the variation in CO<sub>2</sub> levels. This relationship may support the hypothesis that a CO<sub>2</sub>-poor atmosphere is associated with grassland families' geographic expansion and diversification since the Oligocene. Other environmental and biological factors, such as decreasing temperatures and increasing aridity, may also play a role in this process [77]. Around 32 million years ago, a drop in atmospheric CO<sub>2</sub> levels to 550 ppm coincided with the emergence of plants with biological carbon-concentrating mechanisms (CCMs), which are prevalent in today's grasslands and deserts.

The two primary CCMs in land plants, crassulacean acid metabolism (CAM) and C4 photosynthetic pathways, provide competitive advantages over the ancestral C3 pathway, particularly under lower atmospheric CO<sub>2</sub> and low precipitation conditions [51]. Consequently, a negative correlation has been identified between the diversification rates of the grassland families Poaceae and Asteraceae and atmospheric CO<sub>2</sub> levels [77]. If the low levels of atmospheric CO<sub>2</sub> during the Oligocene led to the expansion of more open habitats, this may have favored cursorial species of the Phorusrhacidae family, particularly the subfamilies Psilopterinae and Patagornithinae. Additionally, this environment could have facilitated the emergence of new species with cursorial habits. Based on their body size, it appears that the Phorusrhacinae taxa evolved to occupy the macropredator niche previously held by the Physornithinae, which likely consisted entirely of graviportal taxa [20]. Members of the subfamily Phorusrhacinae are gigantic terrestrial birds but smaller and more slender than Physornithinae. It is composed of *P. longissimus*, which was cursorial, and *D. pozzi* and *K. guillermoi*, which, while both graviportal in proportion, have been suggested to have a superior running ability than Physornithinae [20, 78]. Accordingly, the earliest known and well-preserved Phorusrhacidae footprints indicate that medium-sized species from the Late Miocene (~8 Ma) evolved strong cursorial adaptations [18].

Furthermore, the extinction rate of Phorusrhacidae is positively correlated with the leaf area index, which is a proxy for vegetation openness. Open habitat grasses in southern South America were minor components in predominantly

forested habitats until the early Miocene [72], then grassland radiation favored cursorial terror bird species. However, after the first aridification events of the Miocene since at least 15 Ma, which involved the expansion of grasslands, steppes, and scrublands in South America and a concomitant restriction of forests, rainforests, and wetlands [31], it negatively affected both the more robust and graviportal species, as well as the cursorial species of Phorusrhacidae. In this way, LAI values indicate the presence of dry forest, woodland, or scrubland during the late Oligocene to the early Miocene (~21.1 to 18.8 Ma), when the values decrease, suggesting changes between palm scrub and open forest without a continuous herbaceous understory. Subsequently, in the middle Miocene (~15.7 to 14.6 Ma), a brief increase in the values of this proxy is observed at 14.6 Ma. However, after this, the values decrease again [47]. According to modeling approaches, new xeric biomes are developed by low atmospheric CO<sub>2</sub> levels, decreased temperatures, and increased aridity [77]. Therefore, their development and expansion were favored by events such as the opening of the Drake Passage during the Eocene-Oligocene transition (about 28 Ma), which isolated Antarctica from Patagonia, causing a trend towards colder conditions and the rise of the Andes Mountain range during the Miocene, which blocked the passage of humid easterly winds and induced desertification [14]. In line with the above, osteohistological evidence supports the view that phorusrhacids were very active birds that lacked insularity-related attributes and supports the idea that the extinction of these birds may be related to climatic and environmental changes [79]. Therefore, the presence of vegetation types as well as the

overall composition of vegetation (e.g., providing open or closed habitats) form an important component of the paleoenvironment for these species (e.g., as food or nest resources) and thus play a key role in driving the dynamics of Phorusrhacidae [80].

## **CONCLUSION**

Our findings indicates that the evolutionary history and ultimate extinction of Phorusrhacidae were not the result of a single cause but arose from the intricate interaction between biotic pressures and abiotic processes. Biotic factors, such as increased competition with Carnivora and Didelphimorphia and self-diversity dependence, coupled with abiotic drivers like atmospheric CO<sub>2</sub> fluctuations and the progressive expansion of open landscapes, shaped the group's diversification and decline. Rather than a sudden collapse, the extinction of terror birds reflects a prolonged and multifactorial process, highlighting the vulnerability of specialized apex predators to compounded ecological pressures over deep time.

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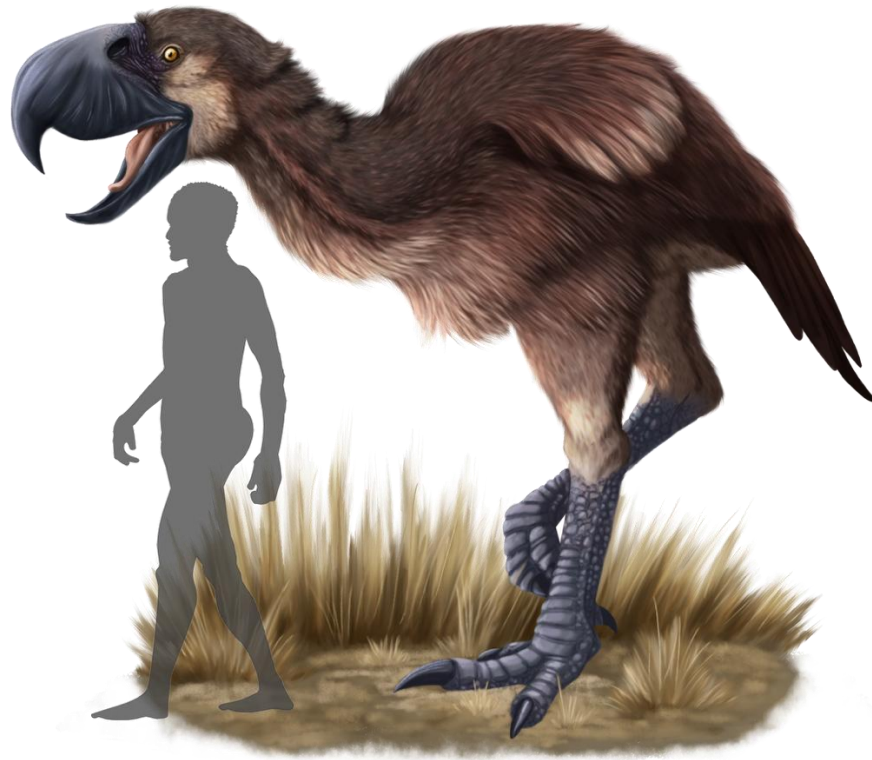
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## ANNEXES

1. *Phorusrhacos longissimus* (Ameghino, 1887) from Santa Cruz Formation (late early Miocene), Santa Cruz Province, Argentina. Scientific artwork by Francisca Zamora-Cornejo (<https://www.instagram.com/pangeaexplora>).

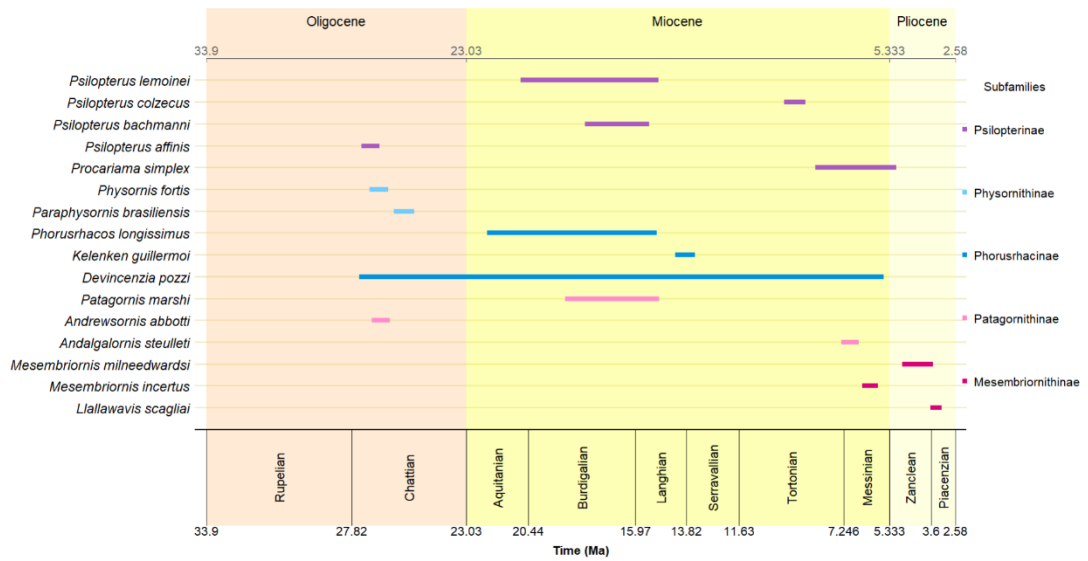


## **2. Databases of fossil occurrences of Phorusrhacidae and competitors**

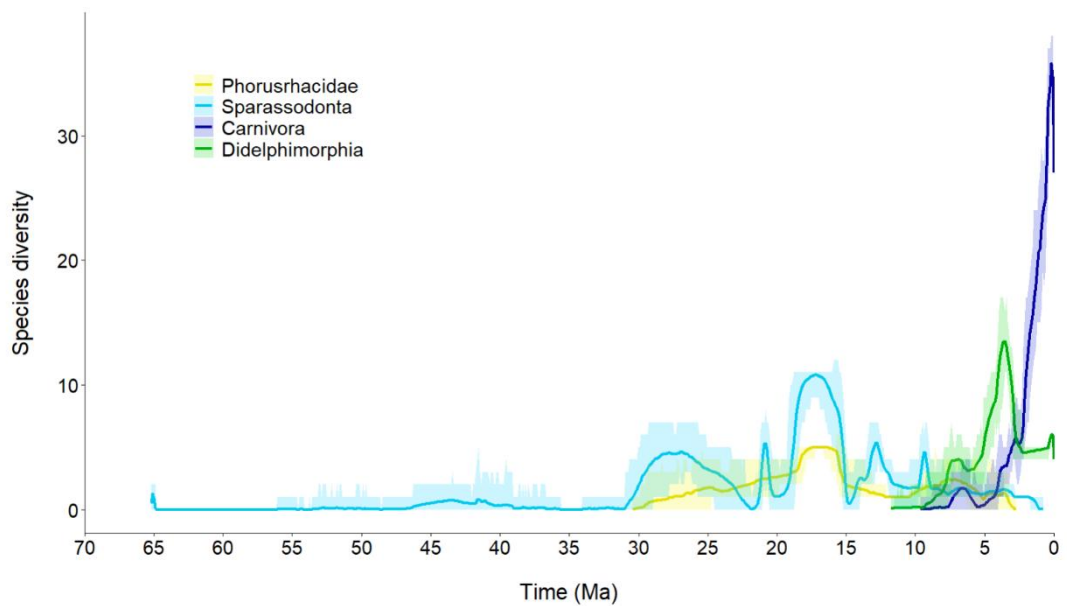
(Sparassondota, Carnivora and Didelphimorphia), and abiotic factors (smoothed mean curve estimated for the entire Andes, paleo-elevation data for the central-southern Andes, leaf area index, proportion of open habitat, mean temperature variation, mean sea-level reconstruction, and mean carbon dioxide levels).

Databases: <https://doi.org/10.5281/zenodo.15313569>

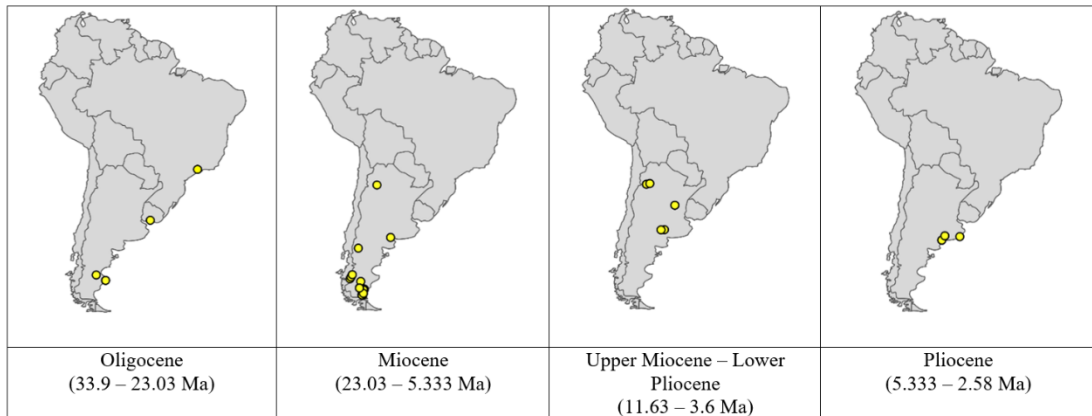
### 3. Supplementary figures.



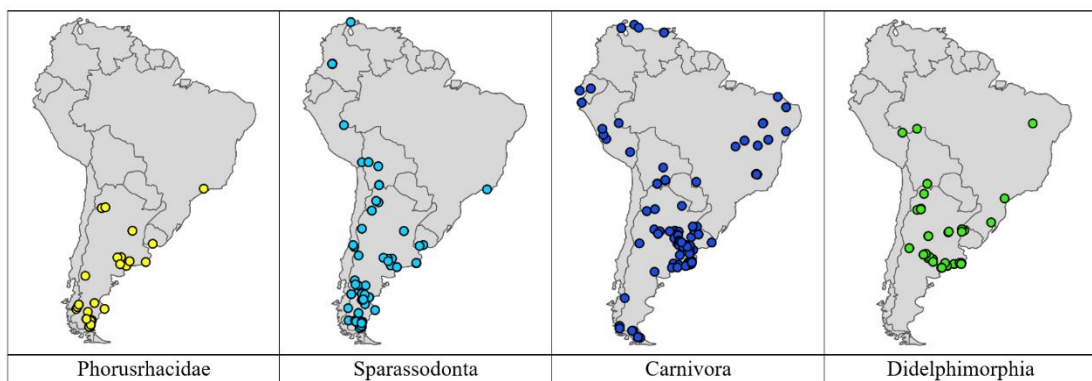
**Figure S1.** Estimated lifespan of each species of Phorusrhacidae, obtained from BDS analyses.



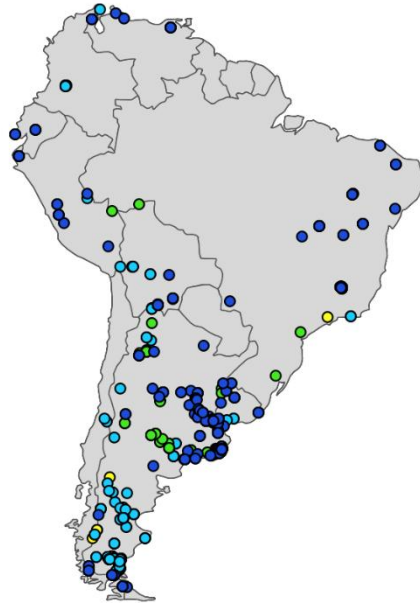
**Figure S2.** Diversity trajectories of Phorusrhacidae and competitors.



**Figure S3.** Presence of Phorusrhacidae occurrences plotted according to epochs, based on the current geographic coordinates of the sampling localities and their age estimates.



**Figure S4.** Presence of Phorusrhacidae occurrences and competitors, based on the current geographical coordinates of the sampling localities.



**Figure S5.** Geographical overlap of Phorusrhacidae and competitors, based on the current geographical coordinates of the sampling localities.

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