

**Main Manuscript for**

The fate of the endemic South American mammal fauna in response to the the most dramatic Cenozoic climate disruption.

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**Author contributions:** L.M., P.O.A. and F.L.C. designed the project; L.B. performed the analyses and wrote the paper with input from all co-authors throughout; all authors contributed to cleaning the fossil occurrence database.

**Competing Interests Statement:** The authors declare having no competing interest.

**Classification:** Biological Sciences, Evolution

**Keywords:** Biological Crisis, Eocene-Oligocene Transition, Faunal Turnover, Mammals, South America

This PDF file includes:

Main text

Figures 1 to 4

Table 1

**Abstract (<250 words)**

Around 34 million years ago (Ma), the Eocene-Oligocene Transition (EOT) marked the most dramatic global climatic change episode in the last 66 million years. Paleontological evidence suggests that this transition was associated with a major faunal turnover, now regarded as a mass extinction crisis in itself at the global scale. However, in South America, there is no consensus on the response of the endemic mammalian fauna to this transition. Here, using an unprecedented fossil dataset and cutting-edge Bayesian methods, we explored the dynamics of South American mammal diversification and their likely drivers across latitude (tropical vs. extratropical), taxonomic groups and trophic guilds throughout the Eocene-Oligocene (56-23.03 Ma). Our results failed at characterizing any mass extinction among South American mammals at the EOT. Instead, they experienced a gradual and long-standing diversity decline from the Early Eocene to the Early Oligocene, followed by a sudden increase in diversity associated with a large taxonomic – but not functional – turnover. Furthermore, tropical and extratropical lineages appear to have very distinct macroevolutionary histories. In particular, no effective change in the pace at which tropical lineages diversify was found, thus favoring the tropical macroevolutionary stability hypothesis. Diversity-dependent effects, temperature and Andean uplift stood out as probable drivers of South American mammal diversification across our study period but, interestingly, not land opening, rejecting the common hypothesis linking Oligocene faunal changes to grassland spreading. Our findings illustrate the uniqueness of the deep-time interplay between the endemic South American mammals and their physical environment in a context of major climatic hinge, highlighting the need for considering regional idiosyncrasies to understand the co-evolution of life and climate.

**Significance statement (<120 words)**

Understanding what drove the apparition and demise of lineages during biodiversity crises will provide key insights at the time of the sixth mass extinction. Here, using an unprecedented fossil database, we explored how South American mammals responded to the most dramatic Cenozoic climate change episode, the Eocene-Oligocene Transition (EOT, *ca.* 34 Ma). We find that South American mammals experienced a gradual and long-standing diversity decline strongly related to Eocene climate cooling, followed by a large taxonomic turnover, driven by diversity-dependent factors and Andean uplift, but not land opening. Therefore, South American mammals were more subject to long-term diversity changes rather than abrupt ones, contrary to what would be expected in a mass extinction scenario.

**Introduction**

Today, South America is home to a unique mammalian fauna, hosting one of the most species-rich regions of the world, the Amazonia [(1)](https://www.zotero.org/google-docs/?5Yguz8). Interestingly, as diverse as it is, the extant mammalian taxonomic diversity is a poor reflection of what can be drawn from the fossil record. In fact, throughout most of the Cenozoic (*i.e.* the last 66 million years), South America was isolated from other landmasses [(2)](https://www.zotero.org/google-docs/?KUdCJq). Therefore, terrestrial mammal lineages present on this continent experienced unique radiations [(3–6)](https://www.zotero.org/google-docs/?nkSXtj). According to ref. [(7)](https://www.zotero.org/google-docs/?uByz0a), South American mammal communities through the Cenozoic are well summarized by three successive ‘faunal strata’. The first one, stretching from the early paleocene (66 million years ago, Ma) to the late Eocene (*ca.* 37 Ma), is characterized by the early arrival and radiation of endemic lineages, mostly xenarthrans, metatherians and native ungulates. Then, from the early Oligocene (*ca.* 33 Ma) until the late Miocene-early Pliocene (*ca.* 5 Ma), key morphological innovations appeared among native lineages, leading to a so-called ‘faunal modernization’ [(8)](https://www.zotero.org/google-docs/?w7ppZz). In the meantime, rodents and primates, immigrant orders from Africa that most likely reached the isolated continent in the middle-late Eocene, diversified locally [(4, 6)](https://www.zotero.org/google-docs/?NleAYR). Finally, this endemic fauna was massively disrupted as the Panama Isthmus closed in the latest Miocene/Pliocene [(9)](https://www.zotero.org/google-docs/?tn2tlm). A large proportion of endemic lineages, such as all native ungulates, many xenarthran or metatherian families, went extinct at that time, meanwhile immigrant taxa from North America, like proboscids, carnivores or artiodactyls, migrated southwards and further diversified, leading what was described as the ‘Great American Biotic Interchange’ [(10)](https://www.zotero.org/google-docs/?57gc1H).

Close to the limit between Simpson’s first and second faunal strata, 33.9 Ma, the Eocene-Oligocene Transition (EOT) marked the most dramatic Cenozoic climatic change episode worldwide [(11)](https://www.zotero.org/google-docs/?TR5V85). At that time, global climate massively cooled down [(12)](https://www.zotero.org/google-docs/?ESBGAD), ocean level dropped [(13)](https://www.zotero.org/google-docs/?4zGJQk), and the whole Antarctic continent turned into a giant ice sheet [(14)](https://www.zotero.org/google-docs/?ZzuvDG). Concomitantly, a major biotic turnover among mammals, known as the ‘Grande Coupure’, occurred in Europe [(15)](https://www.zotero.org/google-docs/?uuc4Hk). This event, punctuated by the arrival of immigrant taxa from Asia, saw the demise of many endemic European lineages [(16–18)](https://www.zotero.org/google-docs/?j5gUkS). Although European-oriented case studies dominate the literature about the topic, similar disruptions among mammalian faunas occurred at the same time in other regions of the world, such as Asia [(19–21)](https://www.zotero.org/google-docs/?l06yd0), North America [(22, 23)](https://www.zotero.org/google-docs/?fBoKUE), Africa [(24)](https://www.zotero.org/google-docs/?BQutKq) or to some extent Madagascar [(25)](https://www.zotero.org/google-docs/?lfRd5b). Recently, ref. [26](https://www.zotero.org/google-docs/?Liuosq) even came to rank this geological boundary as the second most important extinction event throughout the history of life.

In South America, paleontological evidence also suggests a turnover among mammalian communities near the EOT. Substantial changes have been documented among Metatherian [(3, 27, 28)](https://www.zotero.org/google-docs/?aSdWYo) and native ungulate [(8)](https://www.zotero.org/google-docs/?gTxgWt) faunas of central and southern South America. As an echo to the traditional French language expression of ‘Grande Coupure’, ref. [29](https://www.zotero.org/google-docs/?0ldNxW) even came to talk about ‘Bisagra Patagónica’ (*Patagonian Hinge*) to characterize the EOT-related changes among metatherian – and more generally mammal – communities in Patagonia. In northern South America, despite the scarcity of Paleogene fossil-bearing localities so far unearthed, ref. [30](https://www.zotero.org/google-docs/?9iZ8Gr) evidenced marsupial and rodent community changes around the EOT. In addition, general morphological trends were highlighted among ‘modernized’ faunas, with a net increase in herbivore body mass and cheek teeth’s crown height (hypsodonty) [(31)](https://www.zotero.org/google-docs/?m21B82). The case of hypsodonty is particularly interesting, as it evolved convergently in different orders (Notoungulata, Rodentia, Polydolopimorphia, Paucituberculata) from the late Eocene (~38 Ma, 15-20 million years before its first record in North America) and spread during the Oligocene. This key morphological innovation has been primarily associated with a dietary shift toward the consumption of abrasive grasses, hence related to a grassland spreading facilitated by climate cooling and aridification after the EOT [(31–33)](https://www.zotero.org/google-docs/?RQaSSM).

Despite general agreement that a faunal remodeling did occur in South American mammalian communities near the EOT, its evolutionary tempo remains unknown. At macroevolutionary scales, it is unclear whether this faunal renewal was characterized by an extinction of Eocene lineages followed by a diversification of surviving ones, as we would expect in a mass extinction scenario [(e.g. 34)](https://www.zotero.org/google-docs/?Es0qdz), or if lineages transitioned gradually until they become ‘modernized’. A crucial underlying question behind these conflicting macroevolutionary hypotheses is the occurrence, or not, of extinction in the tropics and at which level. Indeed, it has long been postulated that tropics’ climatic stability would make tropical lineages less prone to extinction than extratropical ones [(35)](https://www.zotero.org/google-docs/?kQ7n6w). Also, the ecological selectivity of this apparent faunal transition has remained underexplored to date. Next, the drivers of these biotic changes are still a source of intense debate in the literature. There is no consensus regarding, for instance, the role of temperature [(36, 37)](https://www.zotero.org/google-docs/?bNUoQO) or land opening and grassland expansion [(38)](https://www.zotero.org/google-docs/?7z5Qs8) in shaping these changes. Finally, there is a lack of integrative framework at the continental scale, most case studies being at the local scale, mostly in southern South America. This said, the Paleogene mammal fossil record in South America is spatially and temporally uneven. Spatial gaps encompass immense areas, such as most of the Amazonia, and key time intervals remain unsampled – in terms of fossiliferous regions – including the proper EOT (**Fig. S1** and **3**). Accordingly, it has been historically challenging to tackle questions regarding the history of South American mammals at continental scale.

Here, we intend to fill these gaps by examining the South American Mammal fossil record. We assembled a genus-level fossil dataset composed of 3,384 occurrences (distributed in 1,108 accepted species, 529 genera, 96 families, and 18 orders), ranging from the Late Paleocene to the Early Miocene. Then, relying on a fossil-based Bayesian birth-death framework accounting for variable preservation rates through time and across taxa [(39)](https://www.zotero.org/google-docs/?mfh1XB), we assessed the tempo and modes of mammalian diversification in South America throughout the Eocene-Oligocene (56-23.03 Ma). Afterwards, we disentangled the underlying taxonomic, functional and geographic (tropical v.s. extratropical) bases of the inferred continent-scale patterns of diversity and diversification among South American mammal faunas. Last, we applied a multivariate model to quantify their potential biotic and abiotic drivers.

**Results and Discussion**

***No mass extinction : South American mammal diversity gradually declined well before the EOT***

We analyzed our fossil database at the genus and the species level using the process-based Bayesian framework of diversification inference accounting for preservation implemented in PyRate [(40)](https://www.zotero.org/google-docs/?ZlZ2hk). Our results do not provide support for any mass extinction event having occurred among South American mammal faunas at the Eocene-Oligocene Transition (EOT). Rather, we find that the overall mammal diversity gradually declined from the end of the Early Eocene–shortly after the Early Eocene Climate Optimum–to the end of the Early Oligocene (~30 genera and ~100 species lost), and then further peaked in the Late Oligocene (**Fig. 1D and S8-11**). This diversity trajectory results from a significant decrease in origination rate in the Early Eocene (**Fig 1B and S8-11**). Additionally, we recover a joint significant increase in the pace of origination and extinction (i.e. increased turnover) in the Late Eocene, with the extinction rate always being higher than the extinction rate (slightly negative net diversification rate) (**Fig 1B-C, S8-11**). The same overall diversification pattern is retrieved when analyzing our fossil database at the genus or the species level (**Fig. S8-11**), after removing singletons (**Fig. S12-13**) or disabling several occurrences of the same lineage to co-occur in the same locality at the same time (**Fig. S14-15**). Also, general trends in diversity and diversification are conserved when working with occurrences assigned to South American Land Mammal Ages (SALMAs) (**Fig. S9** and **S11**) instead of Sub-Epochs (cf. Methods and **Fig. S1-2**).

Recently, an analysis of the global Phanerozoic (last 540 My) fossil record classified the EOT as the second most intense mass extinction episode throughout that Eon [(Hoyal Cuthill et al. 2020)](https://www.zotero.org/google-docs/?J6Ps0P). Despite its unexpectedly high ranking compared to other clearly-identified biodiversity crises (e.g. the Cretaceous-Paleogene mass extinction), drastic extinctions at the EOT are supported by analyses of the European [(15)](https://www.zotero.org/google-docs/?XGhvPQ) and Asian [(19)](https://www.zotero.org/google-docs/?uHimsx) mammal fossil record. Recently, applying a methodological framework similar to ours, ref. [18](https://www.zotero.org/google-docs/?uLePND) indeed recovered a strong extinction signal among endemic Western European artiodactyls at the EOT. Here, our results do not corroborate with the occurrence of a mass extinction event among the isolated South American mammal assemblages at the EOT. Rather, we highlight a long-term decline in South American mammal diversity, from the Early Eocene onward, contrasting with the expected short temporality of a mass extinction crisis. To our knowledge, our work is the first to provide quantitative support for such a pattern. As raised by ref. [3](https://www.zotero.org/google-docs/?dXHkFu), a likely explanation for the differences between South America and other continents could come from the isolated condition of the landmass, greatly limiting the possibilities for immigration events, being hypothesized to have played a key role in EOT-related extinctions in other parts of the world.

***Ubiquitous taxonomic – but not functional – turnover among the main mammalian groups across the study period***

Our analyses of the overall South American mammal diversification dynamics failed at characterizing any mass extinction event at the time of the EOT, but recovered a Late-Eocene increase in mammal turnover–joint increase in origination and extinction rates–, followed by a sudden Oligocene increase in diversity (**Fig. 1B** and **D**). As a result, Eocene and Oligocene mammal faunas appear pretty taxonomically dissimilar. Indeed, the proportion of shared genera between each fauna, represented by the Jaccard’s similarity index, is below 20% for four among the five main groups we discuss (**Fig. 1A**). Furthermore, our corrected genus longevity estimates corroborate previously-established results from the literature about mammal taxonomic replacement near the EOT, but also shed new light on previously undescribed patterns (**Fig 1A** and **S18-21**).

Let’s start with notoungulates, the most taxon-rich order of our dataset, encompassing more than a fifth of our total occurrences (**Tab. S1**). Our reconstructions confirm a long-recognized family-level turnover at the order scale between the Late Eocene and the Early Oligocene [(8)](https://www.zotero.org/google-docs/?Wt3dJ8), with the synchronous extinction and origination of respectively three (Archaeopithecidae, Notostylopidae and Oldfieldthomasiidae) and four (Homalodontheriidae, Hegetotheriidae, Mesotheriidae and Toxodontidae) families (**Fig. S19-20**). A fascinating feature in the evolution of notoungulates is that all these newly-arising families, in addition to two surviving ones (Archaeohyracidae and Interatheriidae) convergently evolved larger body sizes and higher teeth crown height (hypsodonty) than their basal counterparts, mostly in the Oligocene (though the first records of hypsodont lineages date back to the Middle Eocene) [(31)](https://www.zotero.org/google-docs/?nmSmpc). As notoungulates likely represented a huge proportion of herbivorous lineages, these innovations therefore suggest huge changes in the architecture of the primary feeder guild between Eocene and Oligocene ecosystems at the continent scale.

If we now focus on the other Native Ungulate orders (i.e. Litopterna, Astrapotheria, Pyrotheria and Xenungulata), apart from the Late Eocene extinction of Trigonostylopidae (Astrapotheria), evidence for higher-level taxonomic changes near the EOT are less obvious (**Fig. S23**). However, there seems to be a strong intra-family taxonomic renewal among most litopterns (i.e. Proterotheriidae, Macraucheniidae, Adianthidae) and astrapotheriids (Astrapotheria) between the Eocene and the Oligocene. Moreover, these groups seem to have been markedly affected by a diversity decline from the Late Eocene to the Early Oligocene (**Fig. S16D-F and S17D-F**). Although their macroevolutionary behavior near the EOT remains greatly less covered by the literature compared to notoungulates’, we could hypothesize that all these changes may have also impacted the structure of herbivorous guilds near the EOT.

In the case of metatherians (**Fig. S18**), our results are perfectly in line with previous findings about their taxonomic renewal near the EOT [(29)](https://www.zotero.org/google-docs/?CBlDCH). On one hand, entire superfamilies or sub-orders like Bonapartherioidea (Polydolopimorphia) or Polydolopiformes (Polydolopimorphia) go extinct in the Early Oligocene, meanwhile others, like Argyrolagoidea (?Polydolopimorphia), paleotenthoidea (Paucituberculata) and Hathliacynidae (Sparassodonta) originate and/or diversify. We might want to precise that, properly speaking, the super-family Palaeotenthoidea appears in the Middle Eocene with the two stem genera *Sasawatu* and *Perulestes*, but the actual Palaeotenthiidae family appears and diversifies in the Early Oligocene. On the other hand, intra-clade taxonomic replacement occurs among Borhyaenoidea (Sparassodonta), Caenolestoidea (Paucituberculata) and Microbiotheria. Ref. [2](https://www.zotero.org/google-docs/?sh8juF)9 established that the most dramatic turnover among metatherian faunas occurred near the EOT, an event they termed ‘Bisagra Patagónica’ (Patagonian Hinge). Our corrected genus age reconstructions clearly bring qualitative support to this view of the metatherian macroevolutionary fate. However, when reconstructing their diversification dynamics throughout our study period, no significant rate shift was found, and the overall number of genera through time remained pretty stable (**Fig 17M-O)**. Hence, quantitatively, our diversification analyses could only provide support for a constant turnover rate across the study period, and the near-EOT interval could not be characterized as a period of increased turnover for metatherian clades. We propose that this might be related to the overall low number of taxa (around 10), possibly hampering the ability for the model to find rate shifts.

As for cingulates, representing the majority of our xenarthran occurrences, we highlight a slowdown in Dasypodinae diversification, meanwhile Euphractinae started to diversify in the middle-late Eocene (**Fig. S21**), as stressed by ref. [41](https://www.zotero.org/google-docs/?VQfxer). This said, in the particular case of Dasypodinae, it is highly probable that this supposed diversification slowdown results more from the incompleteness of the fossil record than from a true macroevolutionary process, given the sparsity of our data and the fact that Dasypodinae is still an extant sub-family.

Finally, when dealing with (caviomorph) rodents, things get simpler (**Fig. S22**). The oldest representatives of the clade are found to originate in the middle Eocene. Then, starting from there, the group diversified at a constant rate (**Fig S16G-I** and **S17G-I**), and no main taxonomic replacement near the EOT is to be noticed.

To track the evolution of functional composition between Eocene and the Oligocene mammal assemblages, we summarized trophic paleocommunities by four dental ecomorphotype-derived categories: herbivorous, carnivorous, insectivorous, omnivorous. Next, we used the origination and extinction ages estimated by PyRate to reconstruct the number of genera through time within each category and further computed the relative proportion of each trophic category at the sub-epoch level. Then, we used these relative proportions to assess pairwise Bray-Curtis dissimilarities between ecological compositions of Early Eocene to Late Oligocene mammal assemblages. Our findings illustrate that the structure of trophic paleocommunities remained pretty stable throughout our entire study period (**Fig. 2**). We report a slight trend toward an increase in the relative proportion of herbivorous lineages in assemblages of decreasing age, at the cost of omnivorous’ and insectivorous’. In addition, ecological dissimilarity increases with the age difference between two assemblages, but remains pretty low (below 25%), in particular between Late Eocene and Early Oligocene assemblages, when it equals 6.1% (**Fig. 2**).

Therefore, our results provide support for a strong taxonomic renewal between Eocene and Oligocene South American mammal faunas, with few changes in the architecture of ecosystems, suggesting strong intra-guild renewal. Interestingly, the timing of the onset of this faunal renewal (Mid-Late Eocene) matches what was established based on the fossil record of benthic foraminifera, gastropods and bivalves, that is “the most fundamental biotic division in the Cenozoic [...] between the middle and the Late Eocene” [(42)](https://www.zotero.org/google-docs/?WkKDtS).

***Diversification histories are heterogeneous across latitudes***

Since the late break-up of the Gondwana supercontinent ~130 Ma, the South American landmass has offered a duality between tropical and non-tropical habitats [(2)](https://www.zotero.org/google-docs/?sXqPCQ). This duality is particularly interesting as it makes it possible to test whether diversification processes occurred the same way in and outside the tropics, a long-standing question in macroevolution [(35)](https://www.zotero.org/google-docs/?JYtdqM). Based on a time series of paleoclimate zone maps [(43, 44)](https://www.zotero.org/google-docs/?xPfs4f), we assigned each of our occurrences a tropical or extratropical affinity (**Fig S3**) and analyzed genus-level diversification dynamics within each biome separately.

Our analyses revealed that extratropical genera exhibited extremely alike diversity and diversification patterns as those obtained from the full dataset across the Eocene-Oligocene (**Fig. 3A-C and S8-11**). Their diversity gradually declined from the Early Eocene to the Early Oligocene, with a Late-Eocene increased turnover (**Fig. 3A-C**). This proximity between extratropical and continent-wide patterns was expected as extratropical taxa account for the majority of genera present in our dataset (85.8%) (**Tab. 1**). Nevertheless, results turn very different when constraining our analyses to tropical genera (**Fig. 3D-F**). Indeed, their reconstructed diversity curve exhibits the exact opposite trend as the one obtained from extratropical genera. Tropical genera diversity increased exponentially in the Eocene, then reached a plateau in the Early Oligocene and fell down in the Late Oligocene (**Fig. 3F**). No significant change was found in the tropical origination rate, but one significant negative shift was found for the tropical extinction rate in the Late Oligocene (**Fig. 3D** and **S24**). We suspect this Oligocene extinction peak and its associated diversity decline to result from the scarcity of low-latitude formations of Oligocene age. In particular, no paleotropical Deseadan (~29.4-24.2 Ma) formation has been unearthed to date [(45)](https://www.zotero.org/google-docs/?N4djqV).

Overall, our results suggest that highly distinct evolutionary regimes shaped tropical and extratropical mammal assemblages in South America. However, there is no clear evidence supporting commonly-assumed macroevolutionary hypotheses regarding how tropics shape diversification processes (**Fig. 3 and S25-S29**). Usually, following ref. [46](https://www.zotero.org/google-docs/?dzjDTZ), people invoke two macroevolutionary scenarios to explain the differences in diversity between tropical and extratropical biomes, that can be drawn both from the present [(1)](https://www.zotero.org/google-docs/?RmiI6S) or the past [(47)](https://www.zotero.org/google-docs/?iuSWWx) of life. On the one hand, tropical lineages would have higher origination rates due to the higher diversity of habitats offered by the tropics (‘cradle’ hypothesis). On the other hand, tropical climate stability would make tropical lineages less prone to extinction (‘museum’ hypothesis). Here, tropical lineages appear to have a higher origination and a lower extinction rate than their extratropical counterparts in the middle Eocene. This would typically be in line with ref. [48](https://www.zotero.org/google-docs/?wX79j9), who reconstructed temporal trends of speciation and extinction rates across latitudes using the mammal tree of life. They found that tropical mammals exhibited a higher speciation and a lower extinction rate than their extratropical counterparts over their evolutionary history. More recently, an emphasis was put on higher extratropical extinctions to explain the build-up of present-day tetrapod diversity [(44, 49)](https://www.zotero.org/google-docs/?P7QRTx). Dispersal rates were also invoked in alternative scenarios aiming at explaining differences between tropical and extratropical diversity [(50)](https://www.zotero.org/google-docs/?beqQJD), although there is no consensus on which of the tropical-to-extratropical [(44)](https://www.zotero.org/google-docs/?IU4T2O) or the extratropical-to-tropical [(49)](https://www.zotero.org/google-docs/?GNa11Q) migrations matter the most. Unfortunately, the absence of a reliable phylogenetic framework encompassing all our taxa, the relatively short time frame we are focusing on and the high spatial incompleteness of our data hampers our ability to reliably explore our data in a historical biogeographic framework.

***Drivers behind the Eocene-Oligocene macroevolutionary dynamics of South American mammals***

Now that we explored the dynamics of South American mammal diversity and diversification throughout our study period, we may wonder what the underlying forces of the trends we highlighted were. In other terms, what drove South American mammal diversity to decline in the 52-33.9 Ma interval? What caused their late-Eocene increase in turnover? How do we explain such levels of taxonomic dissimilarity between Eocene and Oligocene mammal faunas?

Our Multivariate Birth-Death (MBD) analyses indicate that the so dissimilar Eocene and Oligocene faunas were ruled by different drivers (**Fig. 4**). Overall, diversity-dependent effects largely mediated South American mammal diversification history throughout our study period, but these processes shaped both faunas differently. Indeed, we recover strong negative correlations of Eocene (post-EECO, 52-33.9 Ma) origination rate (correlation parameter G𝝀 = -3.24, shrinkage weight w𝜆 = 0.89) and Oligocene extinction rate (Gµ = -2.43, wµ = 0.83) with self-diversity (**Fig. 4, Tab. S3-6**). The first effect suggests that Eocene mammal origination decreased when their diversity increased, which can be interpreted as a carrying capacity effect, that we know can occur at macroevolutionary scales [(51)](https://www.zotero.org/google-docs/?4GXIka). The second one is a bit more counter-intuitive as it suggests that the Oligocene mammal extinction rate decreased when their diversity increased. In line with the taxonomic turnover we previously highlighted, we suggest that it might reflect a facilitation effect.

To investigate these diversity-dependent effects more deeply, we further investigated the effect of genus age on its extinction probability. We splitted our occurrence dataset into two time frames with constant extinction rate (the exact timing of extinction rate shift being estimated with RJMCMC, **Fig. S37-38**). This resulted in an ‘early’ (56-39 Ma) and a ‘late’ (39-23.03 Ma) datasets, respectively containing occurrences preceding and following the late-Eocene increase in turnover we previously discussed. Then, we fitted an Age-Dependent Extinction (ADE) model [(52)](https://www.zotero.org/google-docs/?sykWUT) on each of the two datasets independently. No effect of taxon age could be retrieved from the analysis of the ‘early’ dataset (56-39 Ma), but we found evidence for a significant ADE in our ‘late’ dataset (39-23.03 Ma), with an increasing probability of extinction with decreasing genus age (**Tab. SX**). In the framework of a faunal renewal, we could have expected the opposite relationship, where older lineages would be more likely to go extinct than recently-originated ones. One possible explanation could come from the concomitant increase in origination rate that we discussed previously (**Fig 1B** and **S10A**). The latter would counterbalance the higher prevalence of these newly-originated genera to become extinct, in turn leading to a progressive faunal turnover, as older lineages naturally go extinct. A similar negative relationship between taxon age and extinction probability has been frequently illustrated, for several study models and taxonomic scales [(52–56)](https://www.zotero.org/google-docs/?MwbdGL). Factors proposed to explain this ADE pattern at the genus level often include genus range size, species richness or sampling bias [(53)](https://www.zotero.org/google-docs/?64tvng). In our case, fossil sampling bias is less likely to affect our results as PyRate already accounts for it. In addition, at time of writing, the spatial (**Fig. S3**) and taxonomic (**Fig. S30**) incompleteness of our data do not allow us to reliably test for any of the two remaining factors, but it would be interesting to bear this in mind with the upcoming South American mammal fossil material findings.

Furthermore, we find that global temperature positively correlates with Eocene mammal origination rate (G𝝀 = 0.24, w𝜆 = 0.82). This nicely explains the previously-described gradual decline in South American mammal diversity in the mid-late Eocene, qualitatively matching with the post-EECO decline in temperature [(12)](https://www.zotero.org/google-docs/?lL2u4P) (**Fig. 1D** and **4B**). It is now clearly established that temperature change directly impacts biodiversity, at every timescales [(57, 58)](https://www.zotero.org/google-docs/?ilXkix), and temperature was already identified as a key driver influencing European endemic artiodactyl diversification at the EOT [(59)](https://www.zotero.org/google-docs/?8P8bUs). We should mention that, based on isotope analyses of Patagonian ungulate enamel or on paleobotanical data, authors argued that South American (at least in the Southern part of the continent) climate remained merely stable across the Eocene-Oligocene [(36, 37, 60)](https://www.zotero.org/google-docs/?MKcRW2). However, as illustrated by ref. [(30)](https://www.zotero.org/google-docs/?aQ3jlk), we assume that the spatial scale (i.e. continental vs. global) does not affect the trends and directionality of temperature changes through time, but rather their amplitude. Hence, in the framework of our MBD analyses, the use of a global estimate of paleotemperature is still relevant, as we are more interested in trends than having actual paleotemperature values. In addition, to date, no regional paleotemperature reconstruction for the South American continent has been produced with the same resolution as the global estimate used in this study [(12)](https://www.zotero.org/google-docs/?qcQUjC).

Next, we obtained a weak but significant positive correlation between Oligocene mammal extinction rate and Andean uplift (Gµ = 0.02, wµ = 0.87) (**Fig. 4, Tab. S3-6**). Mountain-building processes are known to greatly influence species diversity (64), and previous studies illustrated the key importance of the Andes in shaping diversity patterns of a wide range of South-American organizms, even in the early stages of the build-up of the chain [(61, 62)](https://www.zotero.org/google-docs/?FsRMqR). Therefore, it makes sense to find a relationship between the pace of Andean uplift and mammal diversification in our study period. In a context of active margin, the Andean orogeny has been associated with volcanic activity. It has been postulated that this activity, in conjunction to subsequent forest fires, resulted in a massive dust emission, in turn promoting grazer-like herbivores origination and diversification, in particular at the EOT and after [(37, 63)](https://www.zotero.org/google-docs/?qxGVVi). Therefore, in the light of these elements, and due to the high proportion of herbivores in our dataset (**Tab. 1** and **Fig. 2**), we could have expected Andean uplift to be either positively related to origination, negatively related to extinction, or both. Here, our results suggest that Andean uplift promoted extinction among South American mammal faunas, thus not providing support for any of the previously-stated hypotheses. Rather, they lead us to hypothesize that the building of the Andes, possibly by fragmenting the landscapes, re-organizing climate advections, triggering volcanism or any other factor, was an obstacle, rather than a facilitator, for Oligocene mammal diversification.

Interestingly, none of our proxies for land opening, *i.e* phytolith-derived floral composition – proxy for grassland spreading, or habitat openness – and relative Leaf Area Index (rLAI) – proxy for forest density – was found to be correlated with any diversification rate. The convergent evolution of high-crowned cheek teeth (hypsodonty) and larger body sizes among several notoungulate families near the EOT, suggesting the emergence of the grazing feeding mode, has long been regarded as an evidence for the expansion of grasslands in response to climate cooling and aridification [(32)](https://www.zotero.org/google-docs/?iH9GN7). However, subsequent studies highlighted that grasslands did not spread that much in the mid-Eocene to Oligocene of Patagonia, meanwhile hypsodont taxa evolved and diversified [(38)](https://www.zotero.org/google-docs/?paCcTs), and more generally, that South American paleo-biome composition remained stable throughout that period [(60)](https://www.zotero.org/google-docs/?92gYia). In addition, trait-based correlation analyses failed at recovering any temporal relation between the evolution of hypsodonty and the abundance of open habitats [(31)](https://www.zotero.org/google-docs/?030SOk). Here, our results for the entire dataset are pointing in the same direction and therefore suggest that mammal diversification was not influenced by the proportion of open habitats in South America. As mentioned earlier, this could be a direct consequence of the apparent biome stability of the continent at that time, and could probably represent one additional feature making the macroevolutionary behavior of South American mammals near the EOT so unique compared to other regions of the world.

When carrying out the MBD analyses without partitioning Eocene and Oligocene faunas, we still find strong negative correlations of origination (G𝝀 = -2.16, w𝜆 = 0.90) and extinction (Gµ = -2.18, wµ = 0.81) rates with self-diversity, and a weak positive correlation of extinction rate with Andean Uplift (Gµ = 0.003, wµ = 0.70) (**Fig. S34, Tab. S3-6**). However, we no longer retrieve any correlation of origination rate with temperature, highlighting the prominent and exclusive role of temperature in shaping Eocene mammal diversity.

***Limits and perspectives***

One of the main limitations of our work surely arises from the fact that many of the taxa we are dealing with (e.g. notoungulates, sparassodonts, glyptodons, ground sloths,...) have no modern representative. This poses a major issue when it comes to making inferences about their ecology as we do not have any proper reference to lean on. It has been suggested that, by many aspects, what we have in the present is insufficient to explain the past of these extinct groups. A great illustration of this is the apparition of high-crowned and/or ever-growing cheek teeth, that many studies – including the present work – failed at relating with grassland spreading, whereas it is known to be the case in the history of charismatic extant groups, such as horses [(32)](https://www.zotero.org/google-docs/?I2pKvJ). Therefore, part of the history of the endemic South American fauna will likely remain an unresolved enigma forever.

Next, as previously mentioned, our data were particularly subject to spatial heterogeneity. For instance, there is a large sampling gap in Amazonia (**Fig. S3**), yet known to be the cradle for most Neotropical groups, ranging from angiosperms to vertebrates [(64)](https://www.zotero.org/google-docs/?OfKUSK). The quasi-absence of fossil mammals from this key region for Neotropical mammal diversification surely hides part of the picture, and even more considering the spatial heterogeneity of diversity dynamics [(65)](https://www.zotero.org/google-docs/?10JGNi). We tried to take this spatial heterogeneity into account in our interpretations as much as we could. Also, we carried out sensitivity analyses to evaluate the extent to which this spatial heterogeneity affected our results, by subsampling our occurrence data to unique taxa-locality combinations, leading to no major difference with the trends we derived from our complete dataset (**Fig. S14** and **S33**).

Apart from space, time and taxonomic completeness were also sources of limitations. As for the former, throughout this work, we saw that many gaps remain in the South American Land Mammal Age scale (SALMA), illustrating the temporal sparsity of the South American mammal fossil record (**Fig. S1**). This surely adds some degree of uncertainty to our taxon age estimations. To intend to cope with this issue, we assigned each of our occurrences with the boundaries of the sub-epoch they most overlapped with (**Fig. S2**). In fact, such an age smoothing did not lead to any major difference in our diversification analyses, likely illustrating PyRate’s ability to deal with data incompleteness. Furthermore, our work also led us to appreciate the unequal representativity of some lineages compared to others, with around 36% of our genera and 54% of our species only represented by a single occurrence in our dataset (*i.e* singletons) (**Tab. S1**). As a result, our average preservation rates per lineages were very low (sometimes less than one) (**Fig. S30-33**), far below the values that we usually see in studies using PyRate [(18, 66, 67)](https://www.zotero.org/google-docs/?d6ItZR). Given this and that the reliability of PyRate has never been tested for datasets exceeding 30% singleton [(68)](https://www.zotero.org/google-docs/?4yS3KA), our results have to be taken carefully. This said, removing singletons did not seem to have any major effect on the inferred diversification patterns (**Fig. S12-13** and **S32**). Overall, despite our encouraging sensitivity tests, we remain conscientious that our dataset largely undersamples South America's past mammalian diversity, and therefore that no statistical framework, as elaborated as it could be, might fully recover the entire picture of its underlying macroevolutionary processes. Further fieldwork will be needed to increase the spatio-temporal and taxonomic completeness of the South American fossil record, and further methodological studies will be required to investigate the impact of such levels of missing data on fossil-based diversification analyses.

Last, a word needs to be dedicated to the reliability of crowd-sourced data, in particular in our framework. Throughout the past few decades, massive efforts have been devoted toward centralizing all published fossil data into large databases (*e.g.* <https://nowdatabase.org/>, <https://paleobiodb.org/>, <https://www.neotomadb.org/>,…). Such an amount of easily-accessible data provided the invaluable opportunity for scientists to investigate large-scale patterns and processes of biodiversity using fossils, the only direct evidence of life in the past. In our case, our primary source of data came from The Paleobiology Database (<https://paleobiodb.org/>). However, we spotted many concerning errors in the raw input data, mostly regarding occurrences’ age or taxonomic name (typos, unaccounted synonymies, missing open nomenclature elements,...). Most of these errors could not have been detected, and further corrected, without the authors’ prior knowledge on the group (see **Fig S2** and **S4**). The need for occurrence data revision was already illustrated by [(69)](https://www.zotero.org/google-docs/?HKDwax), who pointed out significant differences when carrying out diversification analyses from uncleaned and cleaned occurrence data. Therefore, we argue that although powerful statistical tools exist, tackling macroevolutionary issues cannot be done without preliminary biological knowledge on the group that is studied.

**Concluding remarks**

In this work, we studied the macroevolutionary fate of the endemic South American mammals in the Eocene-Oligocene interval. We found no evidence for any mass extinction signal at the Eocene-Oligocene Transition, yet shown for mammal assemblages from other places of the world. Rather, our findings illustrate that South American mammals experienced a gradual and long-standing diversity decline from the Early Eocene to the Early Oligocene, followed by a large taxonomic turnover starting in the Late Eocene and a sharp diversity increase in the Oligocene. Our results also indicate significant differences in the dynamics of mammalian diversity across latitude, with almost opposite trends between tropical and extratropical realms. Diversity-dependent effects, temperature and Andean uplift stood out as likely drivers of South American mammal diversification across our study period. We could retrieve a negative dependency between taxon age and its extinction probability among lineages that originated after the previously-introduced taxonomic renewal. However, due to the numerous gaps existing in the South American mammal fossil record, these findings have to be taken carefully, and further methodological and sampling improvements will be needed to refine them.

**Material and Methods**

***Fossil data compilation***

We first downloaded all Cenozoic mammal occurrences at least with a genus-level resolution from South America on 2023-12-11 (`?base\_name=Mammalia&taxo\_reso=genus&cc=SOA`) (*n=10,440* occurrences). Because diversification regimes do not occur in the same way on land and in the sea [(70)](https://www.zotero.org/google-docs/?YPA3d7), and because the scope of this paper is terrestrial, we removed taxa with marine affinities, *i.e.* occurrences assigned to the orders “Cetacea” and “Sirenia” or the families “Otariidae” and “Phocidae” (*n=354* occurrences). Subsequently, as[(71)](https://www.zotero.org/google-docs/?7G0pGQ) [Tarquini et al. (2022)](https://www.zotero.org/google-docs/?JxEqRO) performed an intensive cleaning of a significant proportion of South American mammalian fossil occurrences (especially Sparassodonts and Native Ungulates), we matched the time ranges of the occurrences we shared with them to those that they proposed (*n=2,998 occurrences*). For the remaining occurrences, we ensured that their time ranges matched the boundaries of their associated interval. For instance, the Mustersan occurrences were all found to be associated with the 48-42 Ma interval. However, radiochronological evidence has shown that this age is younger, constraining its boundaries to 38.2-35 Ma (conservative estimates have even constrained it to 38.2-38 Ma, based on the only clear datations from well-defined levels) [(72)](https://www.zotero.org/google-docs/?gOSR6i) (**Fig. S1**). It is quite concerning to see that such major changes remain uncorrected, especially in public encyclopedies, often used as primary sources of information for non-specialists (e.g. <https://en.wikipedia.org/wiki/Mustersan>). Age boundaries were expressed as either an International Chronostratigraphic Chart (ICC) stage/epoch or a South American Land Mammal Age (SALMA). In the latter case, we used a SALMA scale built *de-novo* based on a literature review (e.g. [Kouvari 2023](https://www.zotero.org/google-docs/?lOroJ8)). Then, based on the literature and the expertise of the co-authors, we manually revised the entire dataset, occurrence by occurrence. This “manual cleaning” aimed at correcting errors in the database, mostly regarding the age range and the taxonomic assignment (e.g. synonymised genus names, typos, missing elements of open nomenclature) of each occurrence (**Fig. S2**). We intended to make this step as clear as possible by documenting most of the changes we made, and why, in the Supplementary Materials. Finally, in order to decrease the number of parameters to estimate, we restricted our dataset to the late paleocene-early Miocene (60-16 Ma). The final dataset comprised 3,384 occurrences, including 529 genera and 1,108 identified species (see **Tab. S1** for a more detailed description of the data).

***Further input treatments***

Subsequent data manipulation and visualisation were carried out using the *Tidyverse* [(74)](https://www.zotero.org/google-docs/?2e0yyd) suite of R packages, the *paleoverse* [(75)](https://www.zotero.org/google-docs/?D4UJRp) and the *deeptime* [(76)](https://www.zotero.org/google-docs/?XNPgAq)R packages. Out of 3,384 occurrences, 2,108 occurrences (representing ~62% of the total) were assigned to a SALMA. Due to temporal gaps in the South American Mammal fossil record this timescale is not continuous (**Fig. S1**). Yet, gaps can highly bias fossil-based diversification inferences, as, for instance, shown in insects [(Jouault et al. 2022b)](https://www.zotero.org/google-docs/?KgAKEV). Therefore, we decided to assign sub-epoch ages to the SALMA-associated occurrences (**Fig. S1-2**), ensuring ourselves to sample the whole study period more evenly.

As illustrated by many studies [(ref. 54, 71)](https://www.zotero.org/google-docs/?gxPBFR), the taxonomic scale has an impact on the diversification patterns we derive from fossil data. Defining species in the fossil record is difficult and prone to debate, and working at the species scale is particularly sensitive to biases such as synonymy or missing open literature elements (e.g. ‘cf.’, ‘aff.’, …). Therefore, we analyzed our mammalian fossil database both at the genus and the species level (**Fig. S2**), but privileged the genus scale for our macroevolutionary conclusions. We further applied several treatments to our data. First, we tested the effect of removing singletons because our genus-level and species-level occurrence datasets respectively comprise 36% and 54% of singletons, i.e. taxa only represented by a single occurrence in the entire dataset (**Tab. S1**). It is worth noticing that including singletons in diversification inferences is still under debate [(34, 78, 79)](https://www.zotero.org/google-docs/?ff3gm7). Also, PyRate was validated using simulated data with a proportion of singletons that, to our knowledge never exceeded 34% [(39)](https://www.zotero.org/google-docs/?03zNAK). Hence, we possibly ignore how the model might behave with such high proportions of singleton as those we have, though it was found to be robust against data incompleteness. Second, we did not allow a given genus (or species) to have geographically and temporally-identical occurrences [(as done by](https://www.zotero.org/google-docs/?iXfOZ1) ref. [34](https://www.zotero.org/google-docs/?x91Vvq)). Next, in order to have a better view on the different tempos of diversification between tropical and extratropical biomes, we assigned each occurrence a tropical or extratropical affinity. Traditionally – both when dealing with extant or fossil lineages – such a geographic splitting is made by defining a latitudinal threshold above (or under, depending on the hemisphere) which occurrences are considered tropical. The latter is commonly set as -23.4° in latitude, but sometimes also -23°, -23.5° or even -30°. However, such a threshold is unsatisfactory, mainly because it does not take into account tropics’ expansions and contractions through geological times (see refs. [44, 49](https://www.zotero.org/google-docs/?jrwUEX) for a discussion on the topic). Therefore, based on their middle age, we binned our occurrences into 5-Myr time bins and reconstructed their paleocoordinates (using the mid age of the bin as reconstruction age) with the PALEOMAP Global Plate Model [(80)](https://www.zotero.org/google-docs/?jqmfvp). paleorotations were produced via an access to the GPlates Web Service (<https://gwsdoc.gplates.org/>) API implemented in the *`paleorotate`* function of the *paleoverse* R package [(75)](https://www.zotero.org/google-docs/?0XxXLN). Then, to assign them a tropical/extratropical affinity, we overlaid these point data with Köppen-Geiger paleoclimate zones produced by ref. [(43)](https://www.zotero.org/google-docs/?ccZlUo) every 5 My (**Tab. 1**). Finally, our fossil occurrence data came with “diet” assignments, derived from dental ecomorphotypes, which we further revised and collapsed to only keep four different classes: carnivorous, herbivorous, insectivorous, and omnivorous (**Tab. 1**).

***Bayesian inference of diversification accounting for preservation***

We used the Bayesian framework of fossil-based diversity and diversification inference accounting for preservation implemented in PyRate 3 [(Silvestro et al. 2014a;b)](https://www.zotero.org/google-docs/?w2v9rn). Relying on birth-death and preservation processes, PyRate jointly estimates the times of origination and extinction and the preservation rate of each taxon, as well as the origination and extinction rates of the underlying birth-death process. We approximated the posterior distribution of each parameter through Reversible-Jump Markov Chain Monte Carlo (RJMCMC) [(68)](https://www.zotero.org/google-docs/?OWtzj1). The RJMCMC algorithm provides an objective estimate of the number of diversification rate shifts, but empirical case studies found that it could also be sensitive to gaps in the fossil record [(Jouault et al. 2022b)](https://www.zotero.org/google-docs/?T44Ns9). Hence, we also analyzed our fossil dataset under a Birth-Death model with Constrained rate Shifts (BDCS) [(81)](https://www.zotero.org/google-docs/?pgOE3t). In the BDCS model, origination and extinction rates can only vary in a piecewise-constant way between a predefined set of time bins. Given the temporal heterogeneity of our data (**Fig. S1 and S4**), this framework was particularly relevant to us because the BDCS model can smooth rates through time when rates are very different within a bin due to preservation issues. We both tested geological stages and 5 My-long intervals as input bins.

To achieve convergence, when working with full datasets, we ran 50,000,000 iterations at the genus level and 100,000,000 iterations at the species level, and sampled every 50,000. When working with taxonomically- or diet-specific datasets, we ran 20,000,000 iterations, sampling every 20,000. For each tested condition, we ran PyRate on 10 or 20 datasets of independently-sampled ages and retained those of which the majority of the parameters (posterior above all) converged. Parameters were considered convergent when their Effective Sample Size (ESS) was above 200. Convergence checks were assessed thanks to the *PyMC* 5.9.2 python library [(82)](https://www.zotero.org/google-docs/?M3CCk9). For each set of runs, burn-in value was specified in an automatised pipeline as the value maximising the ESS of the parameters (choosing between 1%, 5%, 10%, 25% and 50% of the posterior distribution), rather than using the same fixed value every time. Parallel computing was made possible thanks to the *parallel* software [(83)](https://www.zotero.org/google-docs/?ZlYWdf).

In the RJMCMC analyses, we allowed for a minimal time window between two origination/extinction rate shifts of 1 My (`*-mindt 1*`). Setting this value to 0.5 My did not significantly impact the results. We also allowed for preservation rate heterogeneity across taxa (`*-mG*`) as it is more realistic to consider uneven preservations across lineages (some lineages undergo better preservations than others). We set Gamma priors of shapes 1.1 (default value) and model-estimated rates for both origination and extinction rates (`*-pL 1.1 0*` and `*-pM 1.1 0*` options). The preservation rate prior was also sampled in a Gamma distribution of model-estimated rate, but we put a slightly larger shape (`*-pP 2 0*`), offering more flexibility, as done by [Guinot and Condamine (2023)](https://www.zotero.org/google-docs/?aymdGS). We assessed the most suitable preservation model for our data using the maximum-likelihood based model selection test included in PyRate (`*-PPmodeltest*` option), which resulted in favor of the Time-dependent Preservation Process (TPP) model allowing rate shifts between every geological stage (**Fig. S5-S6**). Last, we tested for the sensitivity of our analyses by removing singletons (`-*singleton* 1` option) (**Fig. S12-S13**).

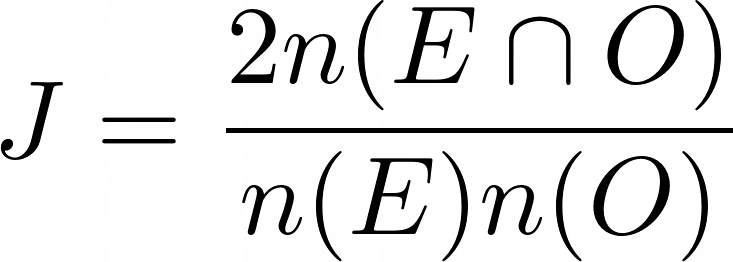
As the BDCS model takes longer to run than the RJMCMC model, we ran the former directly based on the origination and extinction times (respectively *Ts* and *Te*) table estimated with the latter (`*-d*` option). In fact, the joint estimation of *Ts, Te* and the preservation process is the same between both models. What changes is the diversification (birth-death) model they fit to the reconstructed diversity to assess the origination and extinction rates through time (respectively *λ* and *μ*). BDCS models were run across 10,000,000 iterations, sampling every 10,000.

***Age-Dependent Extinction***

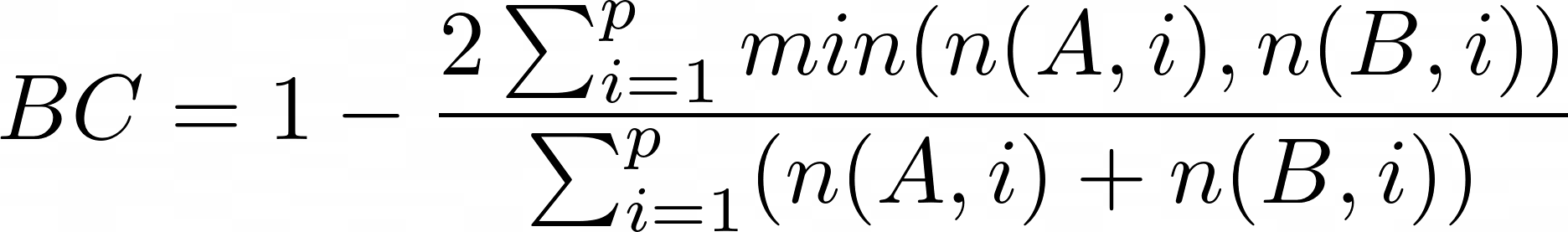
To assess the effect of taxon age on its extinction probability, we fitted the Age-Dependent Extinction (ADE) model to our data (-*ADE 1* option in PyRate) [(52)](https://www.zotero.org/google-docs/?8UHTlT). This model assumes that taxon extinction probability is only a function of its age, and fits a Weibull probability density to the extinction rate de-novo estimated from occurrence data. The presence (or not) of an ADE in our data is given by the value of the shape (Φ) parameter of the Weibull function: if Φ>1, extinction probability increases with taxon age; if Φ<1 extinction probability decreases with taxon age; and if Φ=1, no ADE can be characterized. In practice, we consider that the shape parameter significantly differs from one when one is not included in its 95% HPD. We ensured to fit this model within time windows with a relatively constant extinction rate. As we only retrieved one significant shift in extinction rate around 39 Ma (**Fig 1 and S8-11**), we therefore investigated the effect of the ADE between 56 and 39 Ma, and between 39 and 23.03 Ma (*-filter* option). Just like in the previous section, we set a time-variable preservation process (*-qShift* option) and allowed for preservation rate heterogeneity across taxa (*-mG* option). We ran the model for 40 Million MCMC generations and sampled every 40,000 iterations. Parameters were considered convergent when their ESS was above 200. Convergence checks were achieved using the PyMC3 python library [(82)](https://www.zotero.org/google-docs/?mxx0de).

***Dissimilarity across time among faunal assemblages***

To quantify the extent to which our successive faunal assemblages differed from one another, both in terms of taxonomic and trophic composition, we computed two commonly-used dissimilarity indices to compare ecological communities. We used Jaccard's similarity index to compare the taxonomic composition of the five main mammal subdivisions we defined (notoungulates, other native ungulates, rodents, xenarthrans and metatherians). Considering *n(E)* and *n(O)* the respective total number of taxa within Eocene and Oligocene faunas, and *n(E∩O)* the number of shared taxa between both assemblages, this index is simply expressed as

This index is very intuitive and does not require any knowledge about the abundance of each taxon within both communities. It ranges from zero to one, and the closer it gets to one, the more similar the two assemblages compared are.

Conversely, we compared sub-epoch-level functional compositions of our mammal assemblages by using the Bray-Curtis dissimilarity index, accounting for variations in relative abundance among the four trophic classes we defined based on dental ecomorphotypes (carnivorous, herbivorous, omnivorous, insectivorous). Considering two assemblages A and B, *p* classes (here, *p=4*), and nA,i and nB,i the respective numbers of taxa belonging to the class *i* within the assemblages A and B, this index is expressed as



It also ranges from zero to one, but in that case, values closer to one indicate increasingly dissimilar assemblages.

***Multivariate Birth Death (MBD) model***

To assess the impact of environmental factors on the diversification patterns of South American mammals during the EOT, we ran a Multivariate Birth-Death (MBD) model in PyRate [(84)](https://www.zotero.org/google-docs/?WuKbQf). This model carries out two independent correlations involving a set of environmental covariates (that can be biotic and/or abiotic) and diversification rates newly-estimated from empirical *Ts* and *Te*: one with the origination rate (*λ*), and the other with the extinction rate (*μ*). Each variable is therefore assigned two correlation coefficients, one for the correlation with *λ* (Gi,λ, where *i* is the index of the variable in the set of covariates) and the other for the correlation with *μ* (Gi,μ). An MCMC algorithm jointly estimates baseline origination and extinction rates and all the Gλ and Gµ, while controlling for over-parameterisation. Each Gλ and Gµ is assigned a shrinkage weight (w(Gλ) or w(Gµ)) ranging between 0 and 1, testing its significance–hence, the significance of the correlation itself. A correlation of coefficient Gλ,1 is considered significant if w(Gλ,1) > 0.5 and if the 95% Highest Posterior Density interval of Gλ,1 does not include 0.

We selected 7 abiotic and one biotic variables that appeared relevant to our case study (**Tab. S2**). The abiotic variables included 2 local and 4 local-scale ones. Temperature is known for being a major actor in the diversification of a wide range of clades [(e.g. 58)](https://www.zotero.org/google-docs/?j5Wb2u). Hence, we included in our model the average Cenozoic temperature dataset assembled by ref. [61](https://www.zotero.org/google-docs/?4ZcYDa) using atmospheric δ18O and δ13C records from ref. [12](https://www.zotero.org/google-docs/?feC7ni). In addition, as they are expected to play a key role in habitat fragmentation on macroevolutionary scales, we added the global sea level trends assembled by ref. [13](https://www.zotero.org/google-docs/?WzPKYC) and the average Andean uplift [(85)](https://www.zotero.org/google-docs/?I2xlqc). We also added the Neotropical plant diversity dataset assembled by ref. [86](https://www.zotero.org/google-docs/?SgQZYP). Last, there is a debate regarding the role of land opening in shaping the evolution of South American mammalian faunas, notably among herbivores. We therefore included two regional proxies for land opening: Patagonian patterns of relative abundance of open habitats [(31, 38, 87)](https://www.zotero.org/google-docs/?jK64jG) and Patagonian relative leaf area index [(88)](https://www.zotero.org/google-docs/?u53tm9).

Each abiotic correlate was subsampled or interpolated to a 500 ky time step. In addition, we tested for diversity-dependence effects that could either come from the diversity of the tested clade itself (self-diversity, `*-rmDD 0*` option) or other clades (allowing to hypothesize possible inter-clade interactions). As we expect environmental dissimilarities between the Eocene and Oligocene at the continent scale, especially in high latitudes–where most of our occurrences come from–, we do not expect Eocene and Oligocene faunas to have the same environmental constraints. That is why, in addition to searching for environment signature in the diversification pattern across all our study period, we also decoupled trends among post-Early Eocene Climate Optimum Eocene faunas (51-33.9 Ma), and Oligocene faunas (33.9-23.03 Ma). Each MBD model was run across 10,000,000 iterations, sampling every 10,000. We only carried out exponential correlations (*‘-m 0*’ option). Convergence of the parameters was assessed using the *pymc* 5.9.2Python library [(82)](https://www.zotero.org/google-docs/?KwKUSe), and parameters were considered convergent if their ESS were greater than 200.

A summary of our entire methodological pipeline is provided in **Fig. S2**.

**Data, Materials, and Software Availability**

All the occurrence and outputs data used in this study are available on a FigShare repository (XXX), and all the data analysis and visualisation codes have been deposited in GitHub (<https://github.com/Buffan3369/Neotropical_mammals.git> and <https://github.com/Alexis-Marion/CorsaiR.git> ).

**Acknowledgements**

First of all, we are grateful to all the people who collected and entered the data we used in The Paleobiology Database. Moreover, we thank Chris Scotese and Ignacio Quintero for sharing their tropics-through-time data. Also, we thank Miranta Kouvari for sharing her Master’s thesis work on the South-American eutherian mammal fossil record to study the emergence of the latitudinal biodiversity gradient at the scale of the continent, Alexis F.P. Marion for coding collaborations, and members of the *Phylogénie et Évolution Moléculaire* and *Paléontologie* teams at ISEM for their useful inputs and feedback on the present work. L.B was funded by a grant offered by the *École Normale Supérieure de Lyon*. This is Paleobiology Database publication no. **XXX**.

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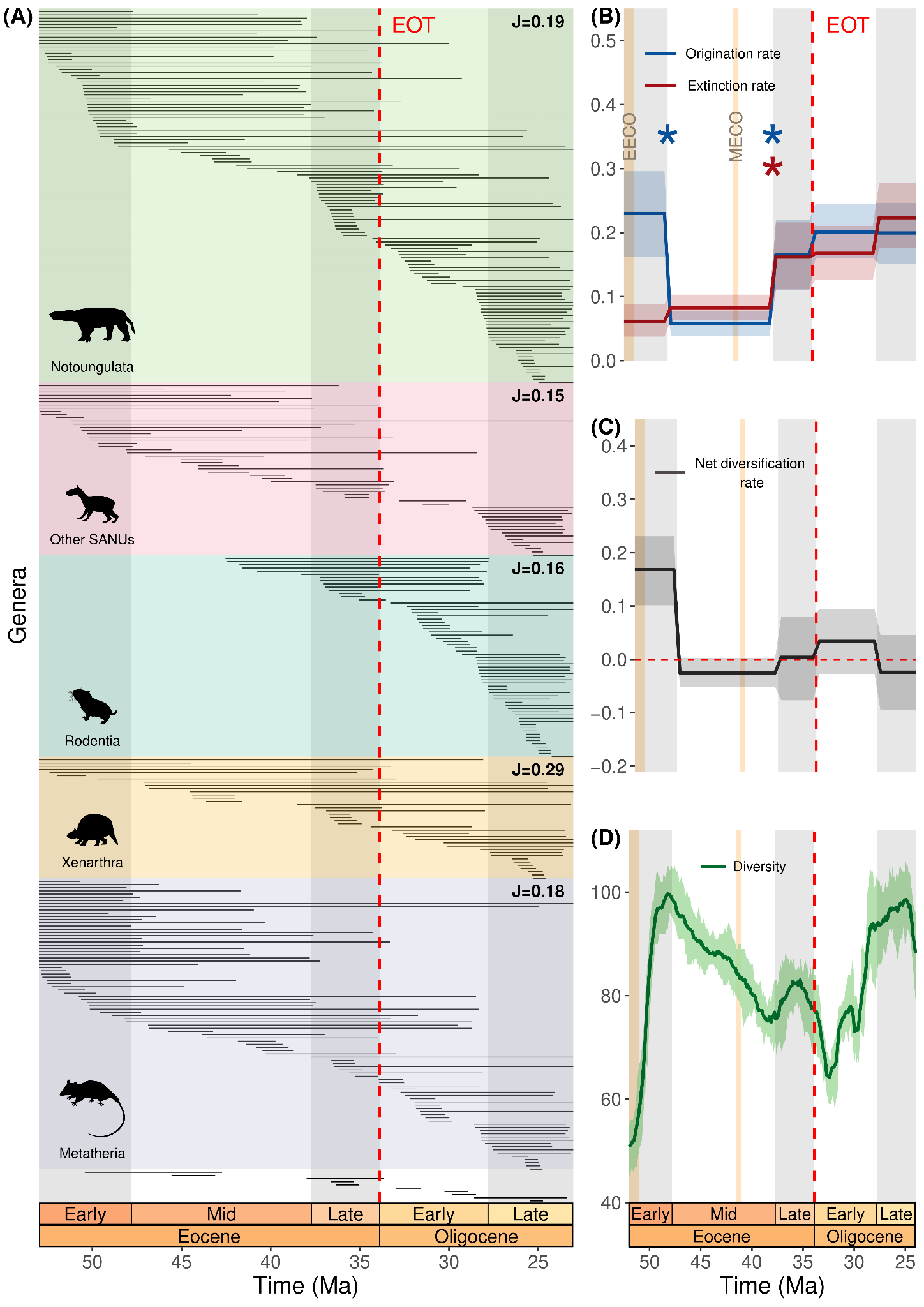
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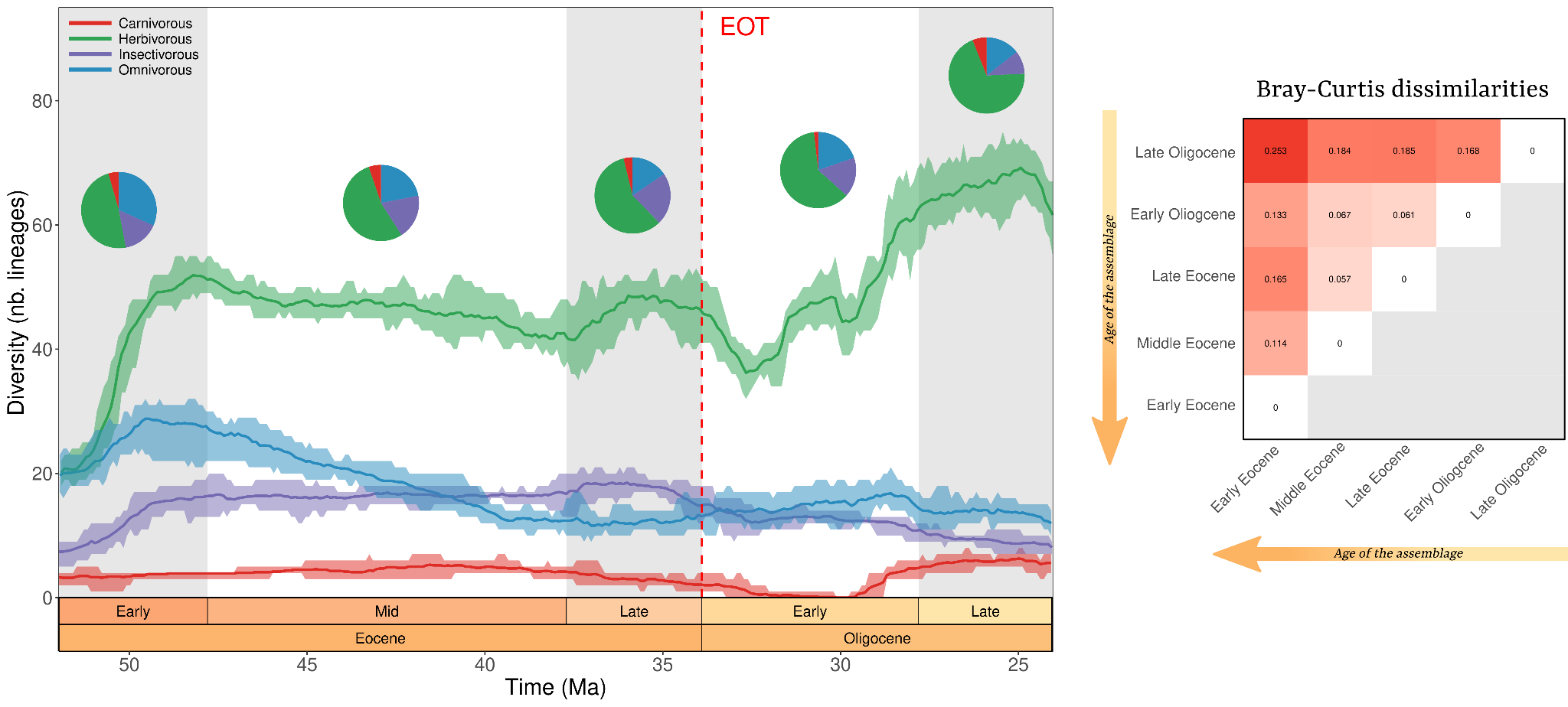
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**Figures and Tables**

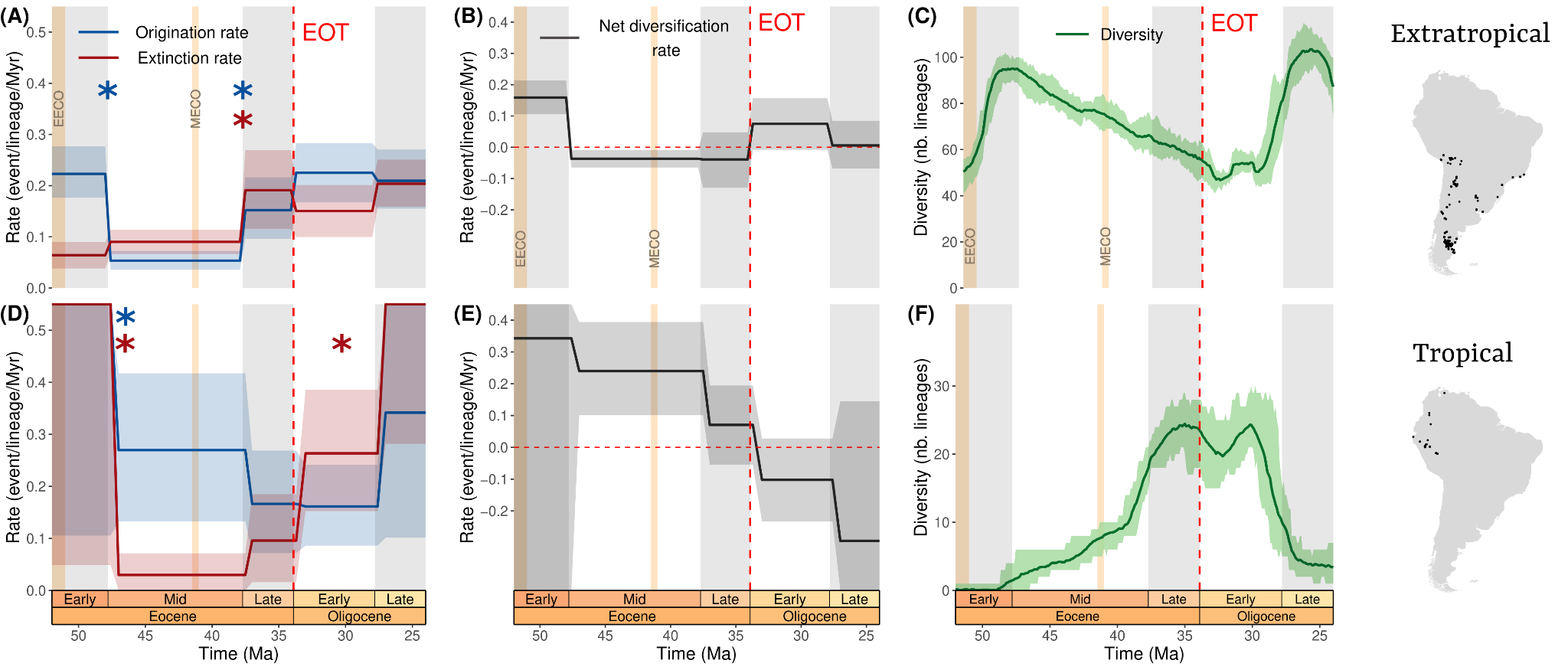


**Figure 1.** Reconstructed longevities (**A**), diversity (**D**) and diversification (**B-C**) dynamics of South American Mammals from the Early Eocene to the Late Oligocene (genus level).

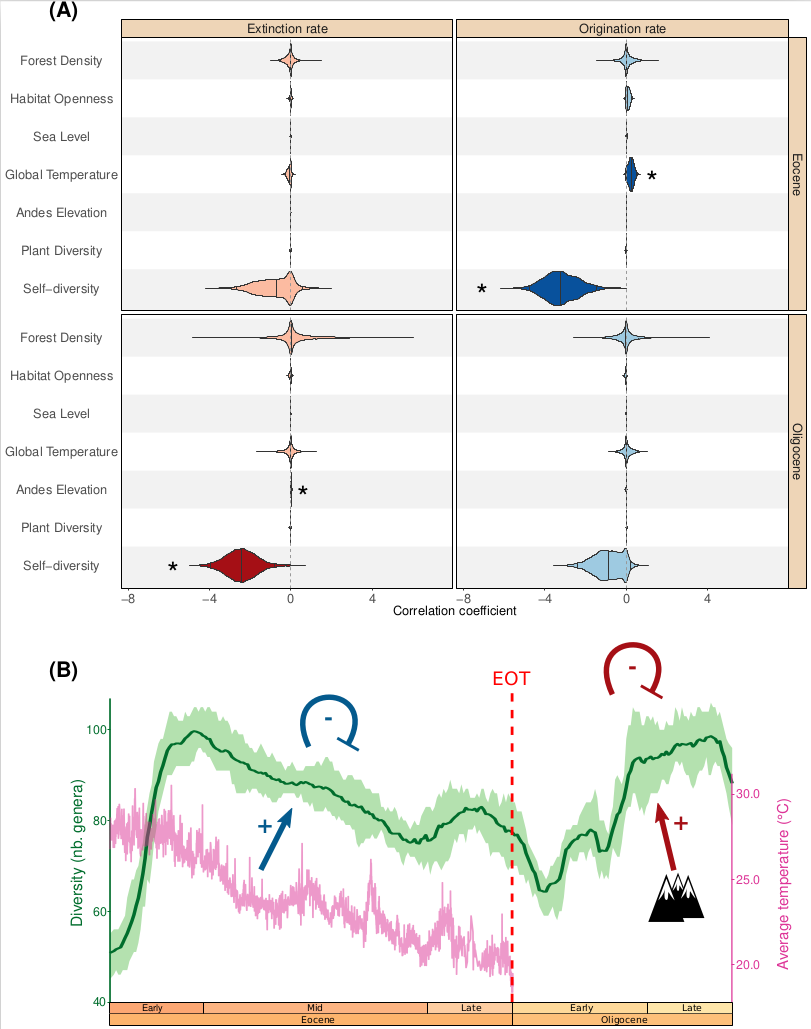
The plot on the left (**A**) shows the longevity–i.e. interval between origination and extinction times–of each Eocene-Oligocene (373 out of 529 genera) South American mammal genus reconstructed by PyRate. J-values are Jaccard’s similarity indices between Eocene and Oligocene assemblages for each of the five groups. The right part of the panel shows the origination (blue) and extinction (red) rates through time (**B**), the net diversification rate (origination-extinction) (**C**), and diversity (**D**) of all South American mammals throughout the study period. Full lines represent median estimates and ribbons their associated 95% higher posterior density. Light brown vertical bands indicate two key climate events, the Early Eocene Climate Optimum (EECO, ~53-51 Ma) and the Middle Eocene Climate Optimum (MECO, ~41.5-41 Ma). Stars on the (**B**) plot indicate significant rate shifts. organizms’ silhouettes are from PhyloPic ([https://www.phylopic.org](https://www.phylopic.org/)) and were added thanks to the R package rphylopic [(Gearty and Jones 2023)](https://www.zotero.org/google-docs/?urTf72)**.** Silhouettes were contributed by Julián Bayona, 2016 (CC BY-SA 3.0), Kai R. Kaspar (CC BY-SA 3.0), Milena Cavalcanti, Patricia Pilatti & Diego Astúa (CC BY 4.0). Geological timescale was added thanks to the deeptime R package [(Gearty 2023)](https://www.zotero.org/google-docs/?HjCXL5)**.**



**Figure 2.** Evolution of genus-level functional assemblages between the Eocene and the Oligocene. The plot on the left shows the median (full line) and 95% HPD (ribbon) of estimated genus richness among the four trophic classes we defined based on dental ecomorphotypes: carnivorous (red), herbivorous (green), insectivorous (purple) and omnivorous (blue). Pie charts indicate the relative abundance of each trophic group for each sub-epoch. The matrix on the right shows pairwise Bray-Curtis dissimilarities between sub-epoch-level trophic communities, with darker colour indicating higher dissimilarities. Geological timescale was added thanks to the deeptime R package [(Gearty 2023)](https://www.zotero.org/google-docs/?KNmLYI)**.**



**Figure 3.** Diversity (**C** and **F**) and diversification (**A-B** and **D-E**) dynamics of South American mammal genera between the Eocene and the Oligocene arranged by paleotropical affinity. Trends are assessed for the extratropical (**A-C**) and tropical (**D-F**) realms. Origination and extinction rates are respectively depicted in blue and red. Stars indicate significant rate shifts. The timing and significance of rate shifts was assessed by the RJMCMC model (**Fig. S37-38**). Their net difference, being the net diversification rate, is represented in black. Diversity through time is plotted in green. Light brown vertical bands indicate two key climate events, the Early Eocene Climate Optimum (EECO, ~53-51 Ma) and the Middle Eocene Climate Optimum (MECO, ~41.5-41 Ma). The maps on the right show the localities of our extratropical (top) and tropical (bottom) occurrences. Geological timescale was added thanks to the deeptime R package [(Gearty 2023)](https://www.zotero.org/google-docs/?6Htihb)**.**



**Figure 4.** Bayesian estimation of correlation parameters on origination (blue) and extinction (red) rates with paleoenvironmental covariates. (**A**) We both considered post-Early Eocene Climate Optimum (52-33.9 Ma, top row) and Oligocene (33.9-23.03 Ma, bottom row) mammal faunas, therefore not treating our dataset as a whole throughout our study period. 2.5%, 50% and 97.5% quantiles are indicated in the distribution of each parameter by vertical lines, respectively from left to right. The interval between the leftmost and the rightmost vertical line of each parameter is therefore its 95% Highest Posterior Density (HPD) interval. Significant correlations, i.e. having shrinkage weights > 0.5 and not including 0 in their 95% HPD are highlighted by stars and darker shades. Details of the environmental variables can be found in **Tab. S2** (‘forest density’ refers to the relative Leaf Area Index, abbreviated rLAI). A graphical interpretation of the highlighted effects of environment covariates on South American mammal diversity is proposed in (**B**). Arrows with a sharp head indicate positive correlations, whereas flat heads indicate negative ones. Just like in (**A**), the colour of the arrow indicates the rate on which the correlation was found, with red being the extinction rate and blue the origination rate. Temperature (displayed in pink) was taken from ref. [12](https://www.zotero.org/google-docs/?PjtsDj).

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
|  | Tropical Affinity | | Dental Ecomorphotype | | | |
|  | Tropical | extratropical | Carnivorous | Herbivorous | Omnivorous | Insectivorous |
| Nb. occurrences | 158 | 3226 | 220 | 2301 | 573 | 290 |
| Nb. Genera | 78 | 470 | 31 | 324 | 116 | 57 |
| Nb. Species | 116 | 1005 | 51 | 698 | 232 | 127 |

**Table 1:** Size of the different climate zones (Tropical Affinity) and diet (Dental Ecomorphotype) categories, expressed in number of occurrences, genera and species.