Palaeoenvironmental constraints on the diversity of eutherian terrestrial mammals through the Cenozoic of South America, and the emergence of the modern-day latitudinal biodiversity gradient on the continent

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I, Miranta Kouvari confirm that the work presented in this thesis is my own. Where information has been derived from other sources, I confirm that this has been indicated in the thesis.

Abstract

South America has a unique geobiological history that is at heightened risk from the current climate emergency. Its fossil record provides empirical evidence of long-term interactions between biodiversity and climate, but our understanding of South America's faunal evolution is still in its infancy. Applying subsampling and Bayesian approaches to a comprehensive dataset of South American terrestrial eutherian mammal fossil occurrences, I demonstrate increases in diversity throughout the Paleogene, resulting from several intervals of high speciation rate. The remainder of the Cenozoic is characterized by greater variability, including a diversity peak in the late Miocene and pulses of heightened extinction rate in the Plio-Pleistocene. These results suggest that the present-day latitudinal biodiversity gradient first appeared in South America in the Plio-Pleistocene, at a similar time as proposed for North American mammals. This appears to have been driven by a decline in mean annual temperatures at higher latitudes in South America, in tandem with an increase in precipitation at lower latitudes that might have been accentuated by Andean uplift in the Pleistocene. Although the Great American Biotic Interchange played a role, Andean uplift appears to have been the primary underlying mechanism driving eutherian diversity patterns in the Cenozoic, radically reshaping the continent's climate and habitats.

Impact Statement

South America is one of the most affected continents from the ongoing climate crisis and biodiversity loss. It also has a unique geobiological history, with the evolution of the Andes greatly influencing regional climate and reshaping habitats, as well as a 55 million-year-long isolation from all neighbouring landmasses, until the formation of the Isthmus of Panama in the Neogene. The continent's mammalian fauna, one of the most diverse today, also mirrors its unique geological and climatic history. It is composed of endemic groups that evolved during its long isolation (including xenarthrans: armadillos, anteaters and sloths), groups that arrived in the

Paleogene (caviomorph rodents, including capybaras, and platyrrhine monkeys), as well as North American emigrants, including mammoths (proboscideans), alpacas, and llamas (artiodactyls), which reached the continent with the formation of the Isthmus of Panama during the Great American Biotic Interchange in the Neogene. South America is an amazing case study of the long-term interactions of biodiversity with climate and habitat changes. However, only a few studies focus on that, especially compared to other continents like North America, that are well studied. Major knowledge gaps still exist, including the impact of geologically long-term climatic change on the continent's mammals.

This thesis aims to fill some of those knowledge gaps and sheds light on the interaction of biodiversity and environment in the last 66 million years. This is done using one of the most comprehensive, and highly curated datasets, that includes the majority of published fossil eutherian mammal occurrences from across South America, and updated geological formation and South American Land Mammal ages, at the time of the analyses. I also utilised palaeoenvironmental data produced by some of the latest versions of the HadCM3 climate models, developed by the UK Meteorological Office. A combination of novel analyses is used to explore the macroevolutionary patters through time and space. The results provide points of comparison with biodiversity patterns of other continents, and can reinforce notions I already had formed regionally, like the appearance of the present-day latitudinal biodiversity pattern that was found likely taking place almost parallel in South America and the neighbouring North America. This thesis also highlights the importance of South American eutherian mammals, that, while representing important stages of eutherian evolution, are not well known to the public, even on that continent (often overshadowed by the popularity of dinosaurs). This thesis provides a narrative of their evolution, that can prove useful for scientific outreach, and public engagement on topics such as evolution, and past climate crises.

The fossil record provides the only empirical evidence of the biodiversity-climate link, and thus these results are relevant not only inside, but outside the academic world. This thesis provides context for the current climate and biodiversity crisis, something that is important for better informed decisionmaking, and policy-designing to tackle the current and future climate crisis and biodiversity loss. Something that cannot be done without the collaboration between the academic and non-academic world.

Acknowledgments

I am grateful to all those that have generated and published on South American fossil mammal data, as well as those that have contributed to incorporating these data into the Paleobiology Database. I thank Lewis Jones for his constructive feedback on the scripts, and his non-stop support, Juan Carrillo for his understanding, patience, and for sharing his expertise on South American mammals and his comments and suggestions on the text. I also thank Grace Varnham for her contribution to data entering South American mammal data in the Paleobiology Database, and Alex Farnsworth, for giving me access to the HadCM3BL-M2.1aD model-produced palaeoenvironmental and topographical data. I thank all the PhD students and post-docs that have been around me and supporting me at Imperial, UCL, the NHM, and outside, and especially Cecily Nicholl, for always being there for me. Finally, I thank my supervisors, Phil Mannion and Anjali Goswami, especially the former, for the support, guidance, and opportunities that they offered me throughout my degree.

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Introduction

We are in the midst of a human-induced global climate and environmental emergency, in which many species are experiencing substantial population declines (Almond et al., 2020; Ceballos et al., 2017) with extinction rates notably higher than those of the past (Barnosky et al., 2011; Ceballos et al., 2015; Pimm et al., 2014).

Species are threatened to extinction, or have already gone extinct locally or worldwide (IUCN, 2020; Wiens, 2016). The impact of global change can also be seen in shifts in the distribution and phenotypes of living organisms in land and water (Blois & Hadly, 2009; Kannan & James, 2009; Parmesan, 2006; Parmesan & Yohe, 2003). In Antarctica, one of the fastest warming places on Earth, ice sheet decrease has led to a chain reaction: a decrease of ocean ice algae led to a decline in krill populations which in turn radically affected the modern distribution of their larger predators (like whales) (Atkinson et al., 2019). In the lower latitudes, the shift of tropical habitats towards more temperate regions (Rajaud & Noblet-Ducoudré, 2017) has led to migrations of tropical insects and birds towards more temperate regions (Paulson, 2001) or to higher elevations respectively (Freeman et al., 2018) in the expense of the faunas already occupying those regions.

Predicted temperature increases of 2–5°C over the next 100 years (IPCC (Intergovernmental Panel Climate Change) Core Writing Team, 2021) reinforces the importance of understanding how biodiversity will respond to climatic changes in order to take appropriate conservation measures. Although these long-term biodiversity responses can be modelled, only the fossil record provides empirical evidence of this relationship between biodiversity and climate (Blois & Hadly, 2009). Climate change is common in Earth’s history and some periods are potentially analogous to those of today e.g. the early Eocene (~50 millions ago; Ma) and the middle Pliocene warm period (~3.3-3 Ma) (Burke et al., 2018). The fossil record is thus especially pertinent given that the accelerating present-day biodiversity crisis will have an impact that extends millions of years into the future (Davis et al., 2018).

Mammals are a taxonomically and morphologically diverse group, with a wide range of sizes, from the Etruscan shrew (weighing only 1.8gr) (Jürgens, 2002) to the largest mammal, the blue whale (~30m in length and weighting ~136,000 kg) (Sears & Calambokidis, 2002). They also take up various important ecological roles in ecosystems (predators, scavengers, seed dispersers etc.) all around the world (Archibald & Rose, 2005; Blois & Hadly, 2009).

Mammals occupy essential roles in ecosystems worldwide but 32% of the 5969 species are in population decline, with 30% identified as at risk of extinction (IUCN, 2020). In particular, ecologically specialised (Brodie et al., 2021) and large-bodied mammalian species (Tilman et al., 2017) are thought to be at highest risk. Climate is thought to have played an important role in the 150 million year (Myr) evolutionary history of eutherian mammals, the group that includes extant placentals, as documented by their remarkable fossil record (Blois & Hadly, 2009; Brodie, 2018; Figueirido et al., 2012; Madden, 1995; Theodoridis et al., 2020).

Of all the continents today, the ongoing climate emergency has the largest documented impact on Central and South American vertebrates, with 94% of species showing population declines over the last five decades (Almond et al., 2020). South America has an exceptional geobiological history, which includes the formation and uplift of the Andes, the longest mountain chain on Earth today, affecting the entire continent’s climate, habitats, and likely driving numerous diversification events over the last 80 Myr (Boschman, 2021; Boschman & Condamine, 2022; Hoorn, Wesselingh, ter Steege, et al., 2010). The continent’s ~55 Myr-long isolation from all neighbouring landmasses (Livermore et al., 2005; Wilf et al., 2013) has led to the evolution an endemic fauna consisting of xenarthrans (sloths, armadillos, anteaters etc.), the now extinct South American Native Ungulates (SANUs), as well as the Paleogene introduction of caviomorph rodents and platyrrhine monkeys, potentially through transoceanic rafting (Antoine et al., 2012; Bond et al., 2015). Isolation ended with the formation of the Isthmus of Panama and the invasion of North American emigrants (including species that are now considered characteristic to the continent, like alpacas and llamas), during the Great American Biotic Interchange (GABI) in the

Pliocene (Carrillo et al., 2020; Cione et al., 2015a; Domingo et al., 2020; Marshall et al., 1982; Morgan, 2008; Soibelzon et al., 2019; Webb, 1976; Woodburne et al., 2006).

Despite South America’s grave present-day situation and exceptional geobiological history, our knowledge of the continent’s faunal evolution is still in its infancy, limiting our understanding of how the present-day distribution of biodiversity was assembled. Major knowledge gaps still exist, including the impact of geologically long-term climatic change on the continent’s mammals.

Most groups of South American mammals are characterized by a latitudinal biodiversity gradient (LBG), in which species richness increases towards the Equator (Fergnani and Ruggiero, 2015; Kaufman, 1995; Stevens et al., 2019; this thesis [Supplementary Information or SI section 14]). Understanding what drives this global, first-order pattern remains one of the great challenges of macroecology. However, a modern-type gradient has not always been present in geological time (e.g. Mannion et al., 2014; Marcot et al., 2016), and it remains unclear when the LBG formed in South America. Consequently, the relative roles of climate, Andean uplift, and the GABI on shaping South America’s LBG have never been tested, but could illuminate our understanding of its emergence. These will be the points of focus of this thesis.

Eutherian mammals

Eutheria (including Placentalia) is the most abundant mammalian group today, the others being Metatheria (including Marsupialia) and Prototheria (including Monotremata) (McKenna & Bell, 1997; Novacek, 1992) (Figure 2 and 3). The definitions of these names have been modified through time but more recently, authors consider Placentalia to include all extant placentals and their most recent common ancestor, whereas Eutheria includes Placentalia and the rest of the extinct mammals sharing a more common ancestor with placentals than with metatherians (Novacek, 1992; Archibald, 2001; Ji et al., 2002; Luo et al., 2011; O’Leary et al., 2013)).

Eutherians differ from the other groups with their relatively long gestation periods and birth of their offspring in a late stage of development (Archibald, 2001). Archibald & Rose (2005) noted that: “Although evolutionary success is a difficult if not impossible concept to define, we believe we know it when we see it. This is the case with the placentals, the clade of mammals to which we belong.” In order to understand how climate influences faunas worldwide, eutherians are a great case to study.

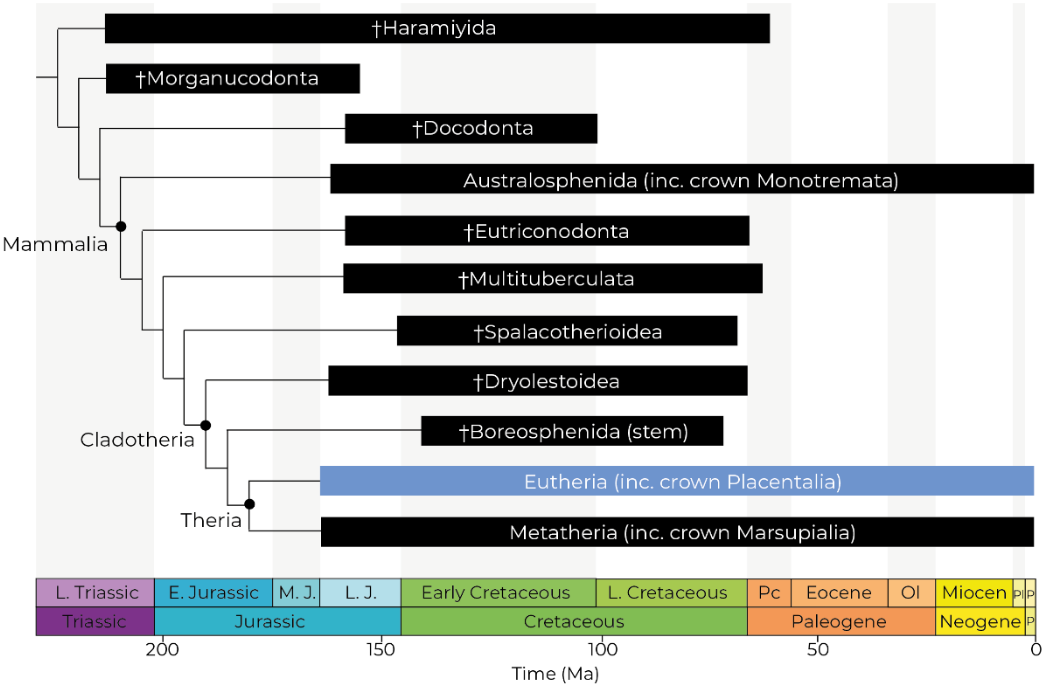

Figure 1: Mammaliaform topology and stratigraphic distribution (bars) of mammals based on figure 1 of (Luo, 2007) except for the first appearance of eutherians and metatherians where the later discovery of *Juramaia sinensis* pushed the groups back to the Jurassic (Luo et al., 2011). L = Late, M = Middle, E = Early

Today’s diversity is just a small part of the group’s evolutionary history. The origin of eutherians and placentals has been pushed back in time with new fossil discoveries (Figure 1 and 2). It was previously thought that the first eutherians dated to the Late Cretaceous with, for example, the discovery of an eutherian-dominated fauna in Uzbekistan (Archibald et al., 1998). However, the first appearance of eutherians has been pushed further back with the discovery of eutherian mammal remains from the Early Cretaceous of China (e.g. Bi et al., 2018; Hu et al., 2010; Ji et al., 2002)) and Mongolia (Rougier et al., 1998). Finally, the discovery of the eutherian *Juramaia* *sinensis*, a fossil specimen dating to 160 Ma from China, pushed back the first appearance of the group to the Late Jurassic (Luo et al., 2011) (Figure 1). Molecular studies showed older divergence times between metatherians and eutherians (e.g. van Rheede et al. (2006), but more recent studies show that Eutheria first appeared 168–178 Ma (dos Reis et al., 2012), thus making molecular results in closer accordance with fossil data. We might still have a long way to go about learning about the first appearance of eutherians; however, we know that eutherian mammals had reached the whole world by the K/Pg boundary, 66 Ma (except Australasia and Antarctica, although these might represent sampling failures, rather than true absences) (Archibald & Rose, 2005).

Similarly, the age of the first placental eutherians has also been a subject to debate. Beck and Lee (2014) put the appearance of placentals in the Late Jurassic to Early Cretaceous, an age considerably earlier than that proposed by other molecular or fossil-based studies. Kumar and Hedges (1998) and Murphy et al. (2001) also put the origin of placentals before 100 Ma. On the other side of the spectrum, O'Leary et al. (2013) propose a post K/Pg origination of placentals (Figure 1 and 2). However, most studies propose a Late Cretaceous origin for placentals, more or less close to the K/Pg boundary (examples Archibald (1996), Springer et al. (2003), Bininda-Emonds et al. (2007), Kitazoe et al. (2007), Wible et al. (2007), dos Reis et al. (2012) and Upham et al. (2019)). In any case, at 65-45 Ma most placental orders appeared and by the early Eocene all modern placental orders (along with their various functional adaptations) were already established (dos Reis et al., 2012; Rose, 2006).

In South America in particular, we have fossil remains of mammaliaforms and mammals from Chubut, like the ichnofauna from Santa Cruz, dating back to the Middle Jurassic (Casamiquela, 1961), as well as *Asfaltomylos* and *Henosferus* (Martin & Rauhut, 2005; Rauhut et al., 2002; Rougier et al., 2007) and *Condorodon* (Gaetano & Rougier, 2012) dating back to the Late Jurassic. Numerous other similar fossils from the Jurassic and Cretaceous have been located around the continent (see Rougier et al. (2021) for a comprehensive review), like the non-therian mammal *Vincelestes neuquenianus* (advanced pre-tribosphenic mammal) from the Early

Cretaceous (Bonaparte, 1986), and some dryolestoids endemic to the continent (Pascual & Ortiz-Jaureguizar, 2007).

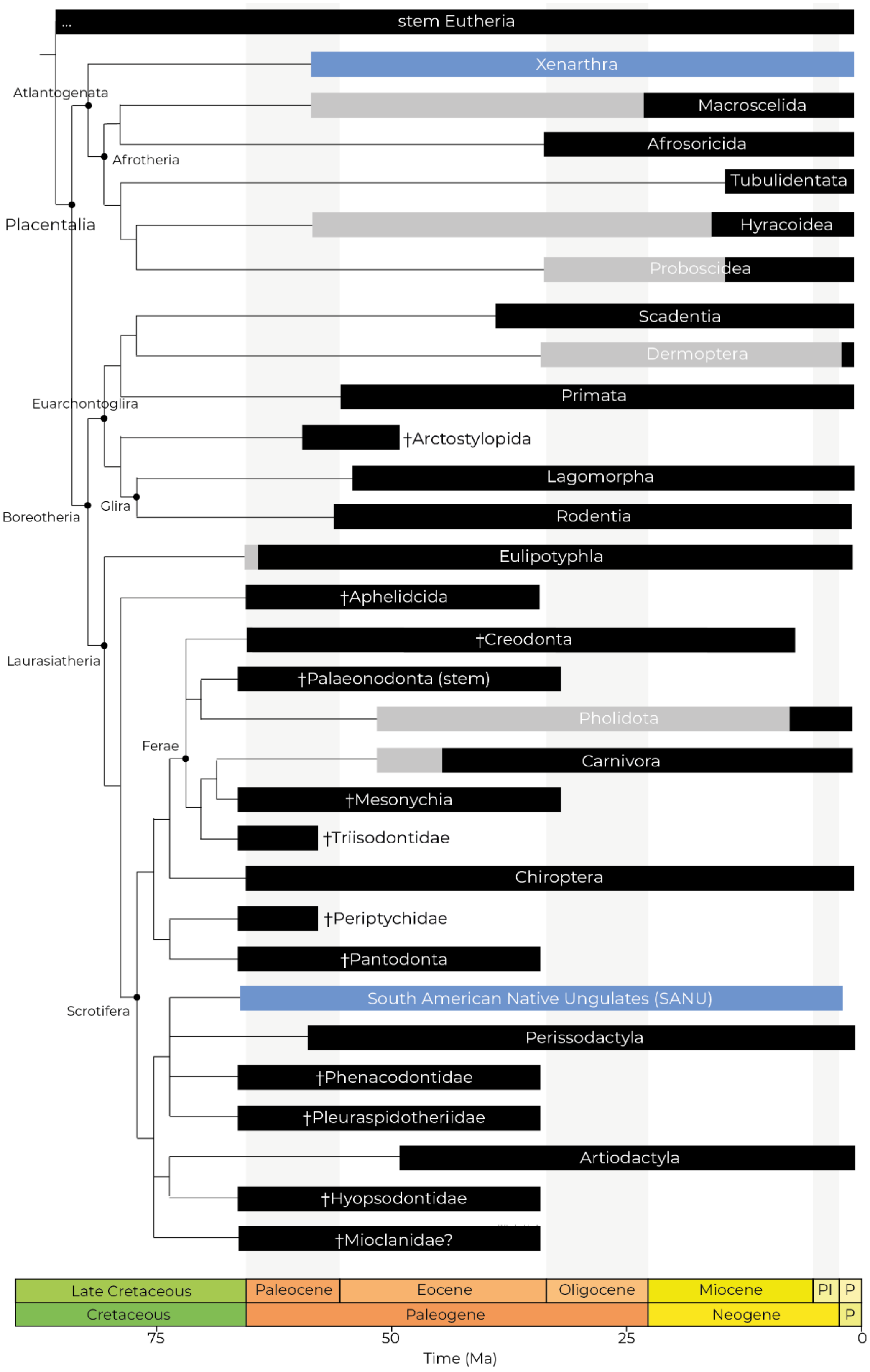

Figure 2: Phylogenetic relationships between Eutheria, and their stratigraphic ranges (bars). The topology of extant placentals follows the molecular analysis of O'Leary et al.

(2013), except for the placental root that was taken from Halliday et al. (2017). According to the latter (morphological analyses with molecular constraints), the early placental split between Atlantogenata and Boreaotheria is supported (instead of an Epitheria/Exafroplacentalia split with a xenarthran root, supported by O'Leary et al. (2013)). The position of the extinct placental clades follows Halliday et al. (2017) except for South American ungulates (grouping Notoungulata, Litopterna and Astrapotheria, sister group of Perissodactyla), the position and topology of which comes from Welker et al. (2015). Stratigraphic ranges of eutherian mammals: For extant groups, the first appearance in the fossil record comes from O'Leary et al. (2013) (for those, black and grey indicate the stratigraphic range of the crown and stem of the group). Stem eutherians last appearance takes place in the Paleogene (Paleobiology Database) but their stratigraphic range might have also extended in the Neogene. The stratigraphic range of Arctostylopidae comes from Cifelli et al. (1989). Apheliscidae have a Paleocene to Eocene distribution Zack et al. (2005) and others. Creodonta (including Oxyaenidae and Hyaenodontidae) have a Paleocene to late Miocene distribution (Gunnell, 1998). Mioclanidae is considered a synonym of Hyopsontidae according to Rose et al. (2012) and the latter have a Paleocene to Eocene distribution (Paleobiology Database). Pleuraspidotheriidae, Phenacodontidae, Palaeanodonta (Paleobiology Database), Pantodonta (Halliday et al., 2017) and Mesonychia (Morlo et al., 2013) also have a Paleocene-Eocene distribution. Triisodontidae and Periptychidae have a Paleocene distribution (Paleobiology database and McKenna and Bell (1997)).

The end of the Mesozoic era

The end of the Mesozoic era, 66 Ma (Renne et al., 2015; Schulte et al., 2010) was marked with the fifth mass extinction (Alroy, 2010c; Benton, 1985; Foote, 2000; Raup & Sepkoski, 1982). Prior to the event, there were no universal diversity patterns: a small decline in diversity was found in pterosaurs (Butler et al., 2013; Longrich et al., 2018), lissamphibians (Close et al., 2020a) and crocodylomorphs (de Celis et al., 2019; Mannion et al., 2015, 2019); however, no similar pattern was found for dinosaurs (Chiarenza et al., 2019; Fastovsky et al., 2004; Mannion et al., 2011; Upchurch et al., 2011). The fossil record of other groups, such as lepidosaurs, is not good enough to permit robust inferences of diversity shifts (Cleary et al., 2018).

During this extinction event, non-avian dinosaurs, pterosaurs, plesiosaurs and mosasaurs went extinct, along with ammonoids, belemnites and other important invertebrate groups (Archibald, 1996; Bambach, 2006; Macleod et al., 1997; Novacek, 1999). As for the groups that persisted into the Cenozoic, some declined in diversity – for example squamates (Longrich et al., 2012), insects (Labandeira et al., 2002) and plants (Vajda & Bercovici, 2014; Wilf & Johnson, 2004). Others seem to have been less affected – for example turtles (Ferreira et al., 2018; Lyson et al., 2011) and crocodylomorphs (Brochu, 2003; Mannion et al., 2015).

Eutherians and metatherians increased in diversity worldwide, relative to other mammalian groups, in the last stages of the Cretaceous (Bennett et al., 2018; Grossnickle & Newham, 2016; Grossnickle & Polly, 2013; Halliday & Goswami, 2016; Williamson et al., 2014; Wilson, 2013; Wilson et al., 2012). This seems to have been followed by a decline in mammalian diversity through the K/Pg boundary (Alroy, 1999; Longrich et al., 2016; Wilson, 2013).

That time was characterised by Pangean breakup, and a series of land bridges connected some of the continents during the Late Cretaceous (Figure 3). South America was still connected to North America (as well as Antarctica and Australia) (Wilf et al. (2013) and references therein). Two migration episodes took place in the continent, with a ~9 million year (Myr) gap in between, during the latest Cretaceous and earliest Paleogene: the “Gondwanan episode” including very brief non therian radiations, and the following “South American episode” (Pascual & Ortiz-Jaureguizar, 2007).

Although there has been some older evidence of therian and tribosphenic mammals in the continent (*Ameghinichnus paragonicus* from the Late Jurassic, found along with fossils of the oldest found tribosphenic mammal in the continent (Rauhut et al., 2002), it is considered that the first therian mammals reached South America during the latter event, reaching the continent through North America. This event has also been called the ‘First American Biotic Interchange’ (FABI) (Goin, et al., 2012a) (Figure 6), and probably included multiple immigration events and a subsequent radiation (Gelfo et al., 2009) that resulted in the decline of all non-therian mammals present there (Goin, et al., 2012a), although some survived until later, e.g., *Greniodon* from the early-middle Eocene of Chubut (Goin, et al., 2012b) and

Necrolestes from the early-middle Miocene (Averianov et al., 2013; Chimento et al., 2012; Rougier et al., 2012)

South America became isolated from North America swiftly after the event, while it remained connected to Antarctica (and Australia) until the formation of the Drake Passage in the Eocene (see dedicated section). The South American faunas evolved in this isolation until the reconnection with North America via the Isthmus of Panama, when the Great American Biotic Interchange (GABI) took place ~ 5 Ma (see dedicated section).

The onset of the Cenozoic

The Cenozoic has also been considered as the “age of mammals” because of the explosive radiation and diversification of mammals characterising that era (Marshall, 1982; Rose, 2006; Simpson, 1937). More specifically, a very important eutherian diversification took place during the early Cenozoic, with the occupation of niches previously taken by dinosaurs, but recently vacated following the K/Pg mass extinction event (Kemp, 2005; Luo, 2007). An exceptional increase in eutherian diversity, body size and functional adaptations of eutherians took place during the Paleocene (Alroy, 1999; Archibald & Deutschman, 2001; Benson et al., 2016; Close et al., 2017; Emerling et al., 2018; Grossnickle & Newham, 2016; Halliday et al., 2016, 2019; Halliday & Goswami, 2016; O’Leary et al., 2013).

While the Cretaceous had higher concentrations of CO_2, a warmer climate (Beerling et al., 2002; Royer, 2006) and a weak latitudinal temperature gradient (Huber et al., 2002; Wolfe & Upchurch, 1987), the Cenozoic (~66 Ma till today) is characterised by climate cooling that followed the Paleocene-Eocene Thermal Maximum (PETM; see dedicated section), and the transition from a greenhouse world to an icehouse world that started during the Eocene-Oligocene (~33.9 Ma) with the formation of permanent ice-sheets in both poles (Westerhold et al., 2020; Zachos et al., 2008) (Figure 3).

The Paleocene/Eocene Thermal Maximum (PETM)

At the Paleocene/Eocene boundary, 56 Ma, a negative excursion of $\delta^{18}O$, shifts in Mg/Ca ratios recorded in benthic and planktonic foraminifera and biomarkers (e.g. leaf margins and oxygen isotopes on fish scales and mammal teeth) show a rapid global warming event of ~5-8 ^{o} C leading to a temperature maximum (of the whole Cenozoic, worldwide). This event is called the Paleocene-Eocene Thermal Maximum (PETM) (Fricke & Wing, 2004; Sluijs et al., 2006; Tripati & Elderfield, 2005; Weijers et al., 2007; Westerhold et al., 2020; Zachos et al., 2003, 2006, 2008) (Figure 3). This was coupled with a carbon cycle perturbation (McInerney & Wing, 2011) and with the lowest equator-to-poles temperature gradient of the past 55 Myr (Moran et al., 2006; Westerhold et al., 2020). This event was relatively short (Jaramillo et al., 2010; Westerhold et al., 2009), ~150-170 kyrs warming event. A longer 5 Myr max warm period – sometimes called Early Eocene Climatic Optimum or EECO followed (Kennett & Stott, 1991; Mudelsee et al., 2014; Stott et al., 1990).

A gradual global cooling followed the EECO event (Passchier et al., 2013; Westerhold et al., 2020; Zachos et al., 2008) and was marked with the replacement of early Cenozoic mammal faunas with “modern” ones, from the Paleocene to the Eocene transition (Janis, 1993; Prothero, 1994) (Figure 3). The Eocene is characterised by two phases of cooling separated by the Middle Eocene Climatic Optimum (MECO) that took place ~ 40 Ma (Miller et al., 1987; Mudelsee et al., 2014; Tripati et al., 2005) (Figure 3).

Intense global cooling continued at the Eocene/Oligocene boundary (see examples of local studies: Schouten et al. (2008); Hren et al., 2013)), in parallel to the forming of the Drake Passage 41 (Scher & Martin (2006); see dedicated section and Figure 3), but also the Tasmanian Passage 33.5 Ma (Kuhnt et al., 2004), resulting in formerly isolated deep cold Arctic waters entering the Atlantic (Potter & Szatmari, 2009). The continuing global cooling is also linked with the appearance of permanent ice-sheets in Antarctica (Miller et al., 1987; Mudelsee et al., 2014; Prothero et al., 2003). This event includes the Early Oligocene Glacial Maximum (EOGM) that took place ~33.7 Ma and was followed by a partial recovery period of relative warm conditions (Zachos et al., 1996).

The fossil record shows evidence that this abrupt and short global warming event, as well as the following cooling, had an impact on the faunas and floras of that time globally (e.g. Wing et al. (2005) for plants, and Currano et al. (2008) for insects). Unfortunately, while the fossil record indicates the appearance of modern mammalian clades like Artiodactyla, Perissodactyla, and Primata, and important dispersions during that time (Blois & Hadly, 2009; Gingerich, 2006), our knowledge is mostly restricted to the northern hemisphere, as the southern hemisphere fossil record is scarce (Gingerich, 2006; Rose, 2006).

The formation of the Drake Passage separating South America and Antarctica

The terrestrial fossil record is scarce in Antarctica; however, there is evidence that South America and Antarctica were linked landmasses (Lawver et al., 1992) through the Weddelian isthmus (Reguero et al., 2014) and that it served as an evolutionary centre as well as a stepping stone towards Australia, until its disconnection (Vizcaíno et al., 1998).

Ice-sheets were not present in all of Antarctica either (Dingle et al., 1998; Dutton et al., 2002) and especially the lower latitudes were mostly ice-free till the middle Eocene (Ehrmann & Mackensen, 1992). Barreda and Palazzesi (2007) and Francis et al. (2007), studying the palaeoflora found evidence of a climatic deterioration of Antarctica through the Paleogene and Vizcaíno et al. (1997) show that by the middle Eocene and until the Oligocene, the habitat should have still been suitable for mammals.

All this permitted the dispersion of mammals from South America to Antarctica (and some to Australia as well) (Olivero et al., 1991; Reguero et al., 2002; Reguero & Marenssi, 2010). Most terrestrial mammal fossil remains are found in the La Meseta Formation on Seymour Island and come from the early Eocene (see Carlini et al. (1990); Reguero et al. (2002); Bond et al. (2011) for the first placentals) – the oldest mammal fossil dating from ~55.3 Ma (Gelfo et al., 2015). This fauna is found closely related to that of Patagonia (Reguero et al., 2002; Reguero & Marenssi, 2010) but shows high endemicity (Vizcaíno et al., 1998). Marsupials reached Australia via

Antarctica during the time these continents were linked (Woodburne & Case, 1996) and there is evidence of the South American origin of Australian marsupials (see for example Kirsch et al. (1991); Arnason et al. (2002); Meredith et al. (2008)).

Patagonia (southern South America) transformed from a shallow sea, due to an Atlantic transgression (Scasso et al., 2012; Spalletti & Franzese, 2007), to a series of caldera-lakes, due to the intensified volcanism linked to the later formation of the Drake Passage. The formation of the Drake passage resulted in the separation of South America and Antarctica – the sea floor extension begun ~55 Ma with the gradual transformation of land to a shallow sea, an increase in separation rate ~50 Ma (Livermore et al., 2005) and the complete formation happened ~36 Ma (Barker & Burrell, 1977; Dalziel & Elliot, 1982; Diester-Haass & Zahn, 1996; Ehrmann & Mackensen, 1992; Lawver et al., 1992; Woodburne & Zinsmeister, 1984) (Figure 4 and 5). The Drake Passage led to the development of the Circumpolar current (Livermore et al., 2004) that enhanced the existing cooling, aridification and the rapid expansion of ice-sheets on Antarctica (Goin, et al., 2012a; Passchier et al., 2013). The halt of mammalian dispersion should have followed the early stages of the Drake passage formation (Reguero et al., 2014). On the other side, Antarctica and Australia were separated ~30 Ma (Veevers, 1991) (Figure 4 and 5).

The end of the Paleogene and “the Patagonian Hinge”

The Paleogene/Eocene cooling has been linked to a faunal turnover event called the Terminal Eocene Event or TEE (Blois & Hadly, 2009) that is more traditionally known from Europe and Asia, with studies referring to it as the “Grande Coupure” (“Great Cut”) in Europe (Agusti & Antón, 2002; Kemp, 2005; Prothero, 1994; Rose, 2006) as well as the “Mongolian Remodelling” (Meng & McKenna, 1998). There is evidence of this event also taking place in South America, and it is named “the Patagonian Hinge” (bisagra patagonica, hinge referring to the fauna shift) (Goin et al., 2010) (Figure 4). This is mostly known from the South American marsupial fossil record, from localities such as Gran Barranca in Patagonia (Abello et al., 2018; Goin et al., 2016; Goin, et al., 2012b), where faunas shifted from an omnivorous, insectivorous, frugivorous diet towards herbivory, especially granivory (Goin et al., 2010).

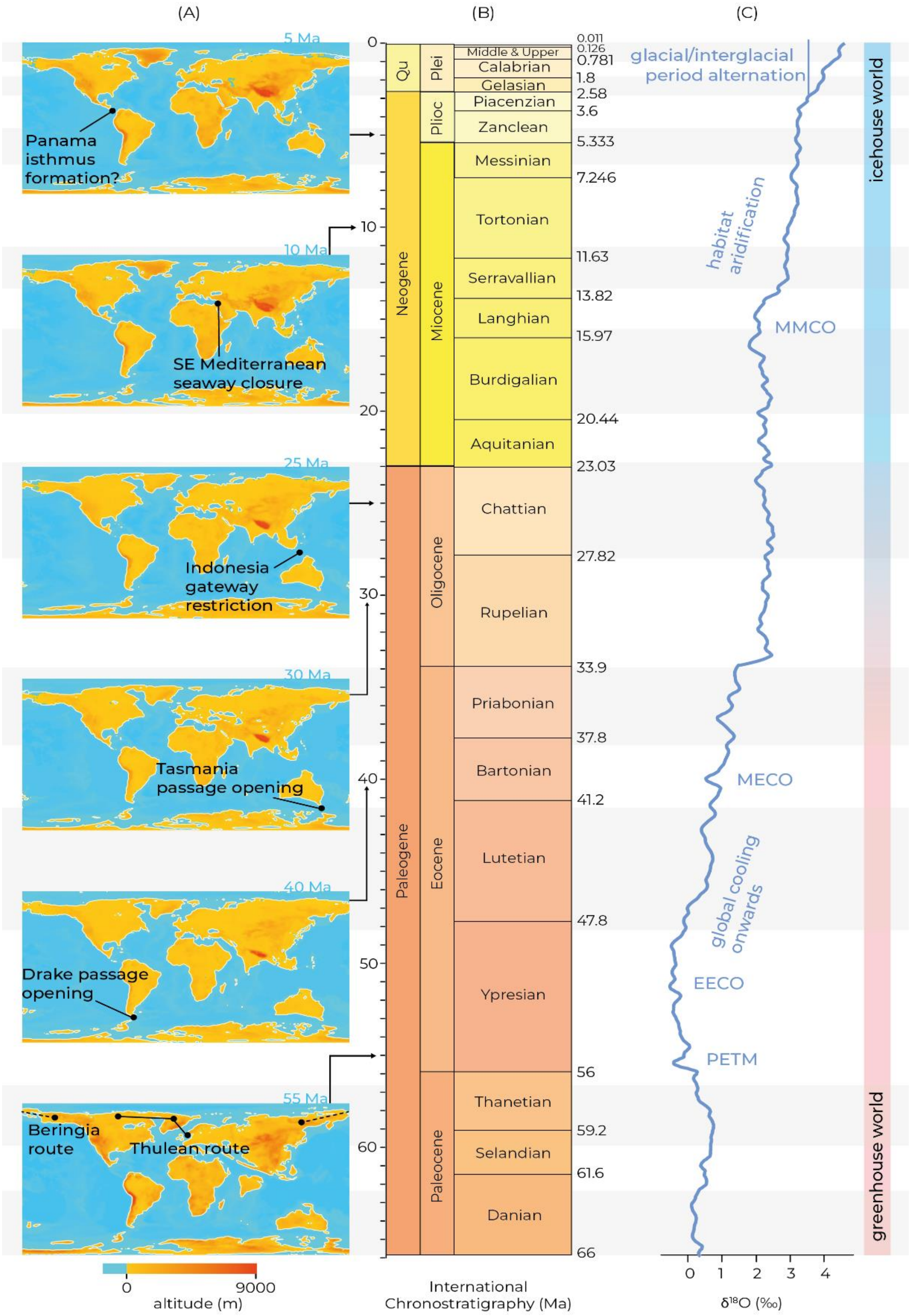

Figure 3: (A) Palaeotopographic maps, constructed in R using Scotese’s Digital Elevation Models (DEM) for every 5 Myr (Scotese, 2001). These models are calculated projections in the past, and can overestimate topography or present more errors, the more those projections go back in time (as seen here for example with the overestimation of altitude in

the Andean region 55Ma). Key palaeogeographic events of the Cenozoic are shown: the Beringia and Thulean route is shown on the map of 55 Ma, the opening of the Drake passage on the map of 40 Ma, the opening of the Tasmania passage on the map of 30 Ma, the Indonesian gateway restriction on the map of 25 Ma, the closure of the South-East Mediterranean seaway at 10 Ma and the formation of the Panama Isthmus possibly around (or after) 5 Ma. Blue hues represent bodies of water (with colour getting darker with depth) and orange/red hues represent land (with red representing higher altitudes). Brikiatis (2014) reviewed the multiple hypotheses on the presence and timing of land bridges and suggested that two land bridges were present during the PETM: the Thulean route (connecting Europe with North America via Greenland) and the Beringia route (connecting East Asia and North America) and the presence of which is also accepted by (Prothero, 1994; Ting, 1998; Agusti and Antón, 2002; Kemp, 2005) and others. The De Geer route linking Greenland with Fennoscandia during the Late Cretaceous, and at the K/Pg boundary the Beringia linking East Asia and North America (Brikiatis, 2014)) between Laurasian palaeocontinents and the beginning of collision of India to Eurasia (Seton et al., 2012). **(B)** International chronostratigraphy (ICS, 2020) in Ma. **(C)** A summary of the climatic changes (Zachos et al. 2008; Westerhold et al., 2020) that took place worldwide during the Cenozoic. All are mentioned throughout the text along with their citations.

The Paleogene ended with the ongoing climate cooling in the Oligocene (Lear et al., 2004; Lyle et al., 2008; Miller et al., 1987; Westerhold et al., 2020; Zachos et al., 2001) and a second glaciation step (or strong glaciation) at the Oligocene/Miocene boundary where the Antarctic ice-cap has already fully formed (Miller et al., 1991; Mudelsee et al., 2014; Shevenell & Kennett, 2007) (Figure 4). The restriction of the Indonesian Gateway (between Borneo and New Guinea connecting Pacific to Indian ocean) took place 25 Ma (Kuhnt et al., 2004) (Figure 5). Now that there is some context on the South American landmass geological and climatic past, it is time to mention more about the actual South American eutherian mammals that are the focus of this thesis.

South American eutherian mammals

The continent's extended isolation led to the evolution of an endemic fauna. The fossil record in scarce on the continent at the beginning of the Cenozoic, it includes, however, key representatives for placental evolution, like the basal pantodont *Alcidedorbignya inopinata* from the early Paleocene of Bolivia (de Muizon et al., 2015). There were two main endemic placental mammal groups, that existed along marsupials that were also endemic to South America throughout the Cenozoic. Those two placental groups were Xenarthra and Meridiungulata or South American Native Ungulates or SANUs (Figure 4).

South American Native Ungulates (SANUs)

Meridiungulata groups all South American ungulates (hooved mammals), of which no representative survives today (Figure 4). This group has been initially thought of as monophyletic (McKenna, 1975; McKenna & Bell, 1997), including the groups Notoungulata, Litopterna, Astrapotheria, Pyrotheria and Xenungulata. However, it is now considered most probably polyphyletic (O'Leary et al., 2013). This group was diverse, comprising a variety of forms such as hippo-like taxa (Toxodontidae (Notoungulata)), animals with a proboscis (*Astrapotherium* (Astrapotheria)) and animals adapted to cursoriality (*Macrauchenia* (Litopterna) (Bond et al., 2001)). However, most groups go extinct in the first half of the Cenozoic. Xenungulates are less known from the fossil record, some of the oldest remains coming from the middle Paleocene (Simpson, 1935), and some of the last in the early Eocene (Villaroel, 1987). Astrapothere fossils come from localities dating from the early Eocene (Kramarz & Bond, 2013; Kramarz et al., 2017; Soria, 1987; Soria & Powell, 1981; Woodburne, Goin, Bond, et al., 2014; Woodburne, Goin, Raigemborn, et al., 2014) to the middle Miocene (Goillot et al., 2011; Johnson, 1984; Johnson & Madden, 1997; Vallejo-Pareja et al., 2015). Astrapotheres (as well as pyrotheres) show adaptations towards large body sizes during that time (Goin, et al., 2012a).

On the other hand, litopterns and notoungulates reach the late Pleistocene, when they go extinct during the megafaunal extinctions of that time (Croft et al., 2020; Goin, et al., 2012a). Litopterns are found in the fossil record from the early Paleocene (de Muizon & Cifelli, 2000; Gelfo et al., 2009), similarly to notoungulates (de Muizon & Cifelli, 2000; Gelfo et al., 2009; Woodburne, Goin, Bond, et al., 2014). Both groups become more abundant in later stages, with last forms like the litoptern *Macrauchenia* (Bond et al., 2001) and the notoungulate *Toxodon* (Barnosky & Lindsey, 2010; Cione et al., 2003) getting extinct in the Late Pleistocene.

Xenarthra

Xenarthra, as the name suggests (strange joints in Greek), differs from the other groups by having more articulated vertebral joints and a very low metabolism (Elgar & Harvey, 1987; Lovegrove, 2000) as well as the presence of osteoderms in some groups (Fernicola et al., 2021). It is one of the earliest diverging placental groups (Meredith et al., 2011), with first representatives dating back to the latest Cretaceous (Delsuc et al., 2016; Gibb et al., 2016; Meredith et al., 2011). Xenarthrans include three main groups: Vermilingua (including extant anteaters), Folivora (including extant sloths), and Cingulata (including extant armadillos). However, today's representatives are just the remnants of a once more diversified group (Figure 4).

Vermilingua are poorly known from the fossil record, with some of the oldest fossils coming from the early Miocene (Carlini et al., 1992), with fossil families Adiastaltidae and Anathitidae represented by very few and fragmentary fossils and so are considered junior synonyms of Myrmecophagidae by McDonald et al. (2008).

Folivora includes arboreal and terrestrial sloths. Today, only two genera survive, *Bradypus* (three-fingered sloth) and *Choloepus* (two-fingered sloths), all small and arboreal. Their fossil record is much more diverse, with fossils dating back to the Oligocene (McKenna et al., 2006). However, their largest diversity comes from the Pliocene and Pleistocene, including giant and small terrestrial forms like *Megatherium* (including *Megatherium americanum* that was weighing >4 tonnes) (Ameghino, 1889; Pujos, 2006; Pujos & Salas, 2004; Saint-André & de Iuliis, 2001).

Cingulata are characterized by having a dorsal carapace made by osteoderms that are usually characteristic of the genus or species (Fernicola & Porpino, 2012). They date back to the early Eocene, with fossils like *Riostegotherium yanei* from Brazil (Oliveira & Bergqvist, 1998) and *Noatherium emilioi* from Argentina (Fernicola et al., 2021). However, as with folivores, the group is mostly known from the Neogene and Quaternary, showing a vast diversity of sizes and specialisations like the heavily armoured glyptodonts, that have been the focus of studies for over two centuries (Ameghino, 1889; McKenna & Bell, 1997).

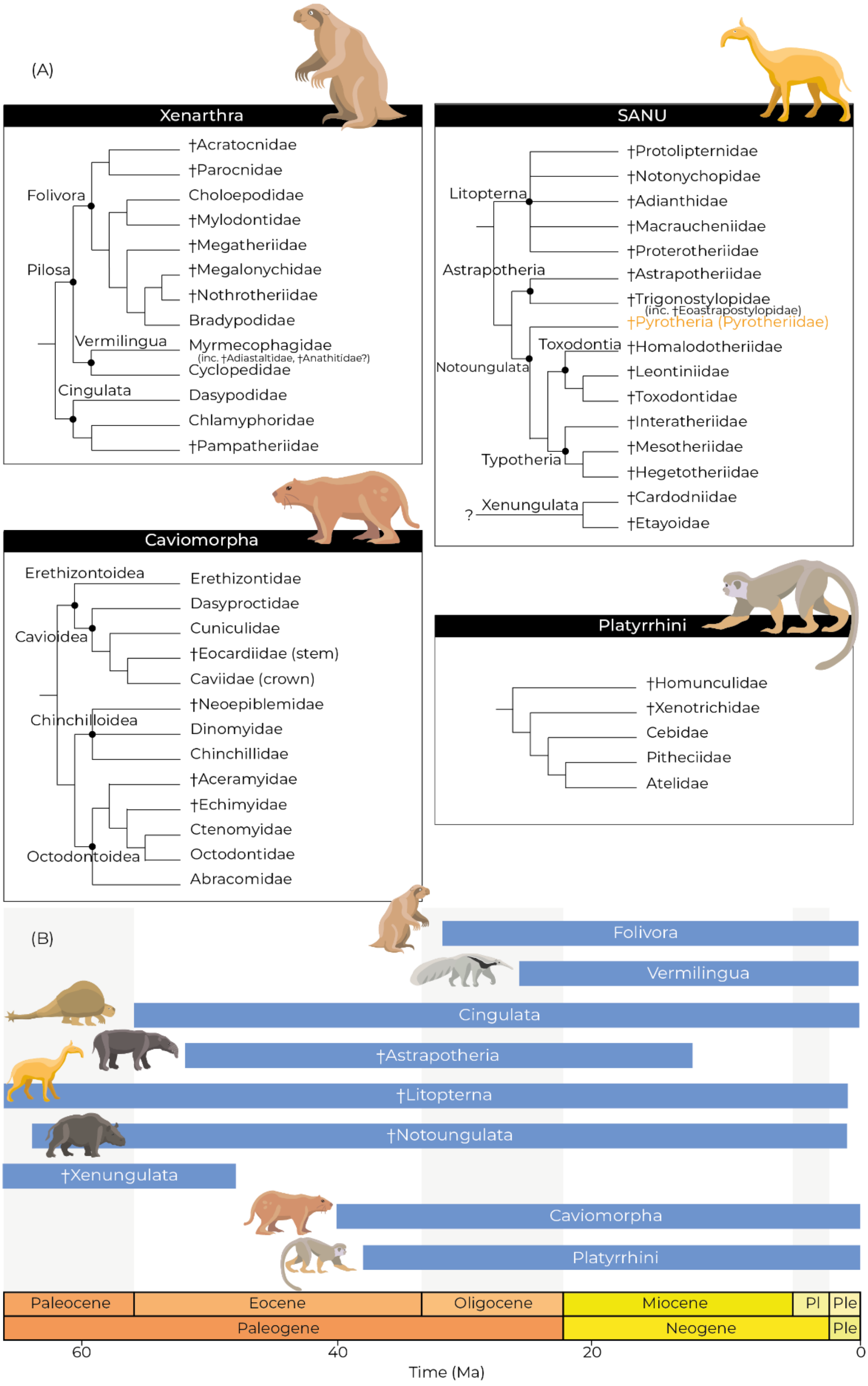

Figure 4: (A) Phylogenetic relationships of Xenarthra, South American Native Ungulates (SANUs), Caviomorpha and Platyrrhini. **Xenarthra**: The general distinction of xenarthrans in Cingulata and Pilosa (including Folivora and Vermilingua) as well as the internal topology

of Cingulata comes from Engelmann (1985); Gaudin (2003); Hill (2005). Topology within Folivora (else called Tardigrada or Phyllophaga) comes from molecular analyses of extinct and extant sloths (Delsuc et al., 2019). Vermilingua (anteaters) are poorly known from the fossil record; fossil families Adiastaltidae and Anathitidae are represented by few and fragmentary fossils and so are considered junior synonyms of Myrmecophagidae by McDonald et al. (2008). **South American native ungulates**: the relative position of Astrapotheria, Litopterna and Notoungulata comes from the molecular analyses of Welker et al. (2015). However, this excludes the Astrapotheria group. De Muizon et al. (2015) support a position of Astrapotheria in closed relation to Notoungulata. Astrapothere internal topology comes from Cifelli (1993), according to which Trigonostylopidae with the addition of Eoastrapostylopidae was the stem group of Astrapotheriidae. Only litoptern monophyletic families were included (Carrillo et al., 2018; Cifelli, 1983; Cifelli, 1993; Forasiepi et al., 2016; Schmidt, 2015). The topology within Notoungulata and the inclusion of Pyrotheria follows Billet (2011). Xenungulata is a poorly known group and only the families Cardodniidae (Simpson, 1935) and Etayoidae (Villaroel, 1987) are known. **Platyrrhini**: The topology of the extant families comes from Wang et al. (2019) molecular analyses. The position of the extinct families was inferred from Kay (2015). **Caviomorpha**: the topology of extant clades comes from the molecular (Bayesian) analyses of Álvarez et al. (2017). The position of Eocardiidae (stem group of Caviidae crown group) comes from Pérez (2010) and the other extinct clades from Arnal & Vucetich (2015). **(B) Stratigraphic ranges (bars) of South American endemic eutherian mammals:** The stratigraphic ranges are based on first and last appearances of the group. The oldest Folivora fossil is a sloth from the early Oligocene (Tinguiririan) (McKenna et al., 2006). The earliest Vermilingua fossil comes from the late Oligocene to early Miocene (Colhuehapian) (Carlini et al., 1992). The oldest cingulate fossils are from the late Paleocene - early Eocene (Itaboraian) (Oliveira & Bergqvist, 1998). Astrapotheres are found from the early Eocene (Itaboraian)(Goillot et al., 2011; Johnson & Madden, 1997; Soria & Powell, 1981; Vallejo-Pareja et al., 2015) to the middle Miocene (Laventan) (Goillot et al., 2011; Johnson, 1984; Johnson & Madden, 1997; Vallejo-Pareja et al., 2015). Litopterns are found in the fossil record from the late Paleocene (Peligran) (Gelfo et al., 2009), but most probably being present from the Tiupampan (de Muizon & Cifelli, 2000) whereas their last appearance takes place in the late Pleistocene (Bond et al., 2001). Notoungulates are recorded from the early Paleocene (Tiupampan) (de Muizon & Cifelli, 2000; Gelfo et al., 2009; Woodburne, Goin, Raigemborn, et al., 2014) until the late Pleistocene (Barnosky & Lindsey, 2010; Cione et al., 2003). The oldest xenungulate fossil comes from the middle Paleocene (Simpson, 1935) and the last known fossil is from the early Eocene (Villarroel, 1987). The oldest age of caviomorph rodents in South America comes from *Cachiyacuy contamanensis* from the middle Eocene (~41 Ma) (Antoine et al., 2012). Finally, the oldest platyrrhine fossil comes from the late Eocene (*Perupithecus* at ~35-36 Ma) (Bond et al., 2015).

Paleogene arrival of Caviomorpha and Plattyrhini

Caviomorph rodents (including extant guinea pigs, chinchillas and capybara) as well as platyrrhine monkeys (including extant capuchins, marmosets and spidermonkeys) are an important part of South America's fauna today. However, these two groups were later introductions to the continent (Campbell et al., 2021; Seiffert et al., 2020) (Figure 4 and 5), presumably reaching South America by rafting across the Atlantic Ocean from Africa (Antoine et al., 2012; Bond et al., 2015; Goin, et al., 2012a).

The introduction of these two groups had been thought to have taken place either as a two-wave radiation with rodents arriving around 34 Ma and primates (Platyrhini) around 28.5 Ma, or as one radiation event (Goin, et al., 2012a; Poux et al., 2006). However, new discoveries have pushed back the first appearance of those groups in South America, with fossils like the caviomorph *Cachiyacuy contamanensis* from ~41 Ma (middle Eocene) from Peru (Antoine et al., 2012), and the platyrrhine *Perupithecus ucayaliensis* from ~35 Ma (late Eocene) from Peru, making the dispersion parallel to the MECO (Bond et al., 2015).

South American Land Mammal Ages (SALMA)

The long isolation and unique geological history of South America, as well as the unique evolution of endemic faunas and floras throughout most of the Cenozoic era, has made it difficult to correlate South American biostratigraphy with that of the rest of the world (Flynn & Swisher III, 1995). However, the high endemicity of those faunas, especially those of placental and marsupial mammals, has been proven useful for biostratigraphic correlations within the continent (Flynn & Swisher III, 1995). These are called South American Land Mammal Ages (SALMAs), are local stratigraphic units that cover most of the Cenozoic era, and that are defined using changes in mammalian faunas (Figure 5B and C). Most of these Ages are informal biochronological units, dated by direct dating of fossils or sediments, and with relating chronostratigraphic sequences in different parts of South America. Their dates have been changed, some more considerably than others, with new studies and methods, allowing updated datings. A more extended literature review of the most up-to-date SALMA limits is found in the SI section 1 of this thesis, and is shown in Figure 5C. In order to make the results of this thesis more comparable to macroevolutionary patterns taking place in other continents, I have "translated" the ages in my dataset, to international chronostratigraphic stages (ICS; see Material and Methods section).

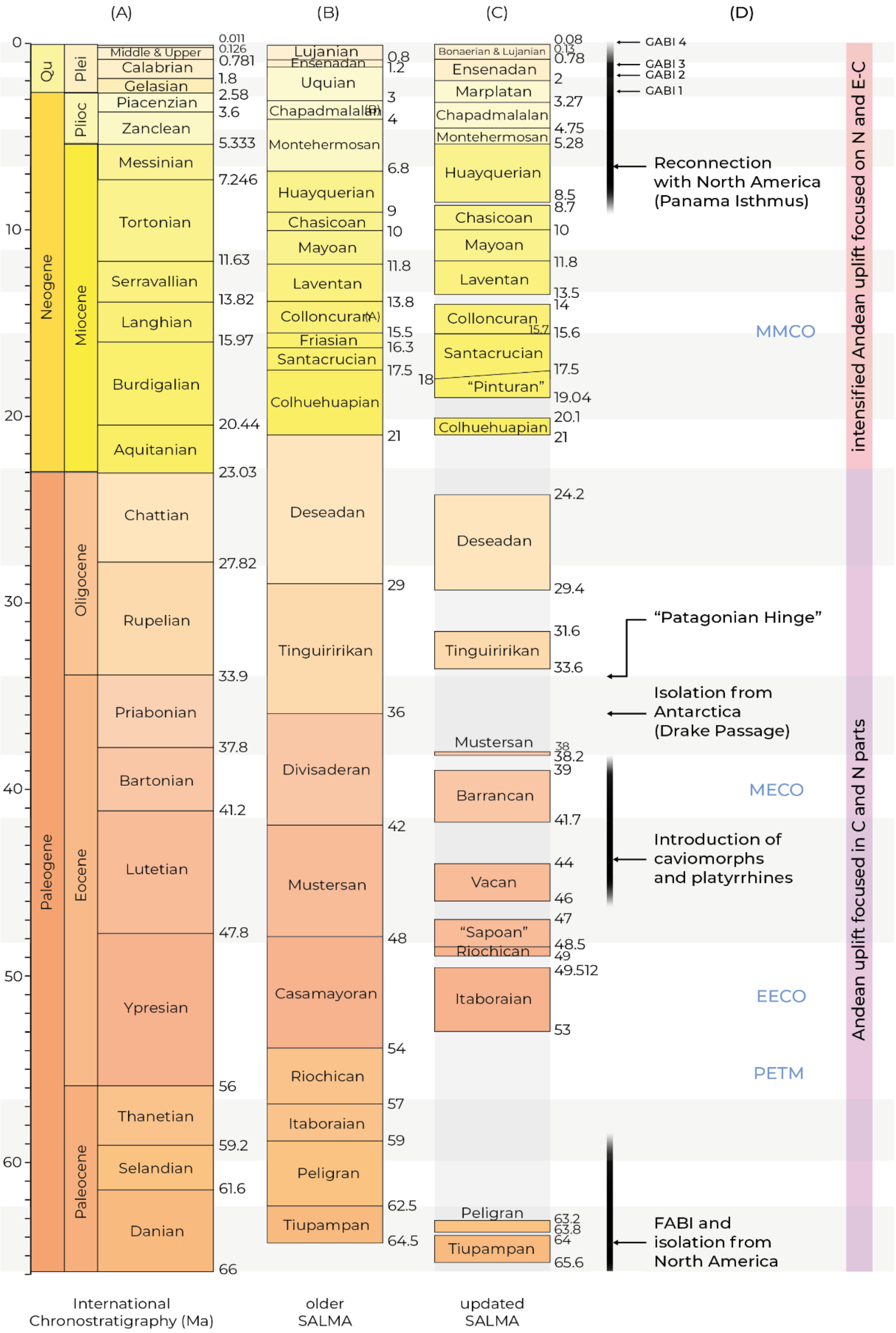

Figure 5: (A) International Chronostratigraphic stages **(B)** older datings of the South American Land Mammal Ages (SALMA) based on (Flynn & Swisher III, 1995), and currently still in use in the Paleobiology Database **(C)** updated datings of the SALMA (see SI section 1 of this thesis for the extended bibliography for these dates) **(D)** A summary of the climatic changes (Zachos et al. 2008; Westerhold et al., 2020) during the Cenozoic along with palaeogeographic and biotic events relevant to South America. All are mentioned throughout the text along with their citations.

Neogene climate cooling and aridification

The Neogene spans from 23 to 2.6 Ma and includes the Miocene (23–5.3 Ma) and the Pliocene epochs (5.3–2.6 Ma; Figure 3 and 5). The increased relative concentration of continents in higher latitudes during the Neogene cooling, coupled with the ongoing climate cooling, assisted the global already present from the Eocene (for example Miller et al. (1987); Wright & Miller (1992); Zachos et al. (2001) and Potter & Szatmari (2009)). Subsequently, the intensification of glaciation followed with the forming of glaciers in Greenland (Thiede et al., 1998) and the westward expansion of the East Antarctic ice sheet (Mercer, 1983). For example, Passchier et al. (2013) found that the inferred mean temperature and precipitation changes in Antarctica coincided with those inferred by vegetation indices and showed a >8 ^{o}C cooling from the Eocene till the middle Miocene.

Notable climatic changes took place in the middle Miocene (Flower & Kennett, 1994; Westerhold et al., 2020; Zachos et al., 2001) and, most importantly, a relatively warm period 17-15 Ma called the Middle Miocene Climatic Optimum (MMCO) (Westerhold et al., 2020; Zachos et al., 2001, 2008) and its subsequent cooling event, the Middle Miocene Climatic Transition (Flower & Kennett, 1994; Mudelsee et al., 2014) (Figure 3 and 5). During the MMCO there is evidence of a less prominent latitudinal temperature gradient (Bruch et al., 2004, 2007). The MMCO signalled an intermediate time of climatic change that was followed by faunal changes worldwide (Blois & Hadly, 2009).

The second half of the Neogene is characterised by the restart of the global cooling trend (Costeur et al., 2007; Legendre et al., 2005; Miller et al., 1991) and Antarctic ice expansion (Shevenell & Kennett, 2007), leading to drier climates (e.g. van Dam (2006); Potter & Szatmari (2009)) (Figure 3 and 5). The closing of the Mediterranean seaway from the collision of Arabia and Asia took place 10 Ma (Rogl, 1999) (Figure 3).

The last stage of the Miocene, the Messinian (7.2–5.3 Ma), is characterised by the intensification of climate cooling and aridification continued and the Mediterranean salinity or Messinian crisis took place, in which the Mediterranean lost contact with the Atlantic 5.6-5.3 Ma because of the brief closing of the Gibraltar passage, thus becoming a hypersaline ‘lake’ (Hsü et al., 1973, 1977; Krijgsman et al., 1999) (Figure 3). The Pliocene (5–3 Ma) had a relative warm period (Maslin et al., 1998; Shackleton et al., 1988) until the onset of the Northern Hemisphere Glaciation (NHG) ~3.2 Ma (Poore & Sloan, 1996) or earlier, ~3.6 Ma (Mudelsee & Raymo, 2005) (Figure 3). Further cooling led to a period with successive glacial and inter-glacial periods (that went on and became the main characteristic of the Pleistocene and Holocene periods) (de Schepper et al., 2014; Hepp et al., 2006). The formation of the Isthmus of Panama resulted in the disappearance of the Equatorial flow that further intensified the global cooling trend (Potter & Szatmari, 2009). By the end of the Neogene, the final environmental, climatic and tectonic changes took place that shaped the world to what we see today – with the exception of the glacial and interglacial iteration of the Pleistocene (Potter & Szatmari, 2009) (Figure 3 and 5).

Habitat shift towards grasslands

Due to the ongoing climate cooling, and potentially the emergence of land during low sea levels (MacFadden et al., 1992), there has been a worldwide expansion of grasslands over tropical and temperate forests (Medeanic, 2002; Retallack, 2001; Velichko, 2005). This has been evidenced by the gradual diet shift in mammal herbivores, containing more and more C_4 grasses, and less C_3 type forest plants ~8–6 Ma, as shown by mostly tooth enamel studies (Cerling et al., 1997; MacFadden et al., 1992). In other words, the gradual replacement of browsers with grazers (i.e. herbivores whose diet includes more than 60% monocotyledonous grasses (Gagnon & Chew, 2000)) takes place, and this was coupled with herbivore immigrations on most continents like Eurasia (Badgley et al., 2005; Fortelius et al., 2006; van Dam, 2006), North America (Barnosky, 2001; Barnosky & Carrasco, 2002; Hopkins, 2007; Janis et al., 2004), Africa (Bobe, 2006), and South America (Flynn et al. (2003); Pascual (2006); see also the Great American Biotic Interchange section, and Figure 3 and 5).

Further increased aridity and continuation of the expansion of grasslands affected Eurasian faunas in the late Neogene (Cano et al., 2014; Cerling et al., 1998; Fortelius et al., 2006; Janis, 1993; van der Made et al., 2006), sometimes in the form of diversity losses (Costeur & Legendre, 2008; van Valkenburgh, 1999), but also dispersions such as the immigration of hippopotamoids, cercopithecoid monkeys and gerbils from Africa to Europe (Agusti, 1999; Agustí et al., 2006; Azzaroli & Guazzone, 1979; García-Alix et al., 2016).

The aforementioned diet shift towards grazing was also coupled with a trend towards hypsodonty (i.e. the presence of high-crowned teeth), that provided increased resistance to dental wear during consumption of more abrasive food, like grasses (Billet et al., 2009; Madden, 2015). Hypsodonty appeared in various placental groups worldwide, like equids and proboscideans in North America, antelopes, hippos, giraffids in Africa, hypsodont deer, hippos and giraffids in Eurasia (Damuth & Janis, 2011; Jernvall & Fortelius, 2002; Kemp, 2005; MacFadden & Ceding, 1994; Strömberg, 2006), as well as notoungulates and rodents in South America (Carlini et al., 2006; Cifelli & Villarroel, 1997). In fact, hypsodonty appeared in South America around 10 Myrs earlier than in the rest of the world, among notoungulate groups of the Paleocene (Gomez Rodrigues et al., 2016; Jardine et al., 2012; MacFadden, 2000; Madden, 2015; Pascual & Ortiz-Jaureguizar, 1990; Stebbins, 1981). It has also been hypothesized that the presence of hypsodonty in South American groups is also linked with the evolution of the Andes, and the increased presence and deposition of detritic particles on plants consumed by these animals (Dunn et al., 2015; Kohn et al., 2015; Strömberg et al., 2013).

While the Plio-Pleistocene also includes further diet shifts (DeSantis et al., 2009), faunal turnovers (Bobe & Behrensmeyer, 2004; Vrba, 1995; Wesselman, 1995) and migrations between continents (Kemp, 2005), the most notable event of this time was the “Great American Biotic Interchange” (GABI), the exchange of mammalian faunas between South and North America with the formation of the Isthmus of Panama (see dedicated section) (Figure 5).

The reconnection with North America, and the arrival of North American emigrants

The South American isolation ended when North and South America were joined by the formation of the isthmus of Panama and the “Great American Biotic Interchange” (GABI) took place (Simpson, 1980; Stehli & Webb, 1985). There have been numerous studies trying to understand the timing and forming of the Panama isthmus. Jaramillo (2017) summarized the main stages in the evolution of the Panama isthmus, starting by the emergence of an “island” in the late Eocene, the product of intraplate Pacific volcanoes in the southern part of the Caribbean plate (Buchs et al., 2011). This was followed by a second terrestrial landscape development in the early Miocene, product of the collision between Panama and South America (Farris et al., 2011) and this region seemed to be connected with North America (Kirby & Macfadden, 2005; MacFadden, 2006; MacFadden et al., 2014) and dominated by tropical rainforest, its presence continuing through the Miocene (Jaramillo et al 2014). In the late Miocene (12–10 Ma) the full closure of the Central America Seaway (CAS) took place (Montes et al 2015) but while the deep water exchange ceased, the shallow sea water exchange continued until the end of the Pliocene (Coates et al., 2004). The last stage that followed consisted of the cessation of shallow sea water exchange and the full and continuous emersion of the isthmus of Panama. Most studies seem to accept this sequence of events, however the timing and importance of those – and especially that of the complete forming of the Panama isthmus – are in debate. Some studies show evidence of a “late” complete formation of the Panama isthmus in the late Pliocene at 2.8 Ma (O’Dea et al., 2016), ~2.5-3.0 Ma (Bartoli et al., 2005), 3 Ma (Jackson & O’Dea, 2013), 3.1 Ma (Keigwin, 1978), 3.1-3.5 Ma (Coates & Obando, 1996), 3.5 Ma (Jaramillo, 2017) and 3.5-4.2 Ma (Jaramillo et al., 2017).

Other studies show an earlier formation of the isthmus in the Miocene at 6-10 Ma (Bacon et al., 2015), 13-15 Ma (Bacon et al., 2016; Montes et al., 2015) and from at least 17.5 Ma (Bacon et al., 2013). Finally, Montes et al. (2012) argue for the initial formation of the isthmus in the middle Eocene/Oligocene.

These researchers debate over the different methods used, but also (maybe more importantly) two key issues exist: the first has to do with the definition of an isthmus and the second about how essential an isthmus is for a faunal exchange to happen. The definition of an isthmus states that it is a continuous strip of land surrounded by water connecting two larger areas of land (Cambridge Academic Content Team, 2020). The problem is that the fossil record does not preserve the whole geological history and does not provide a good temporal and spatial resolution of the events. Because of this, it is very difficult to see the difference between an uninterrupted/continuous strip of land or its occasional interruption by shallow sea water through geologic time. For example, Jaramillo (2017) and Jaramillo et al. (2017) argue that there have been periods of complete absence of shallow sea water in the Panama region and thus argue for an early isthmus formation whereas (O’Dea et al., 2016, 2018) argue that there was a continuous interruption of land by shallow seas until the end Pliocene when the isthmus properly emerged.

The other important point of discussion is that a completely emerged strip of land is not a prerequisite for a faunal dispersal to happen. There are numerous examples of animals and plants colonising close regions separated by water, islands being one example. Consequently, evidence of animals crossing between North and South America is not necessarily evidence for a completely formed isthmus (continuous uninterrupted land) (Bacon et al., 2016; O’Dea et al., 2018), as some studies (e.g., Bacon et al. (2013, 2015)) seem to imply. In any case, the above studies seem to accept the presence of terrestrial animal immigrations before ~3 Ma (with or without the presence of a fully formed isthmus) and the intensification of the interchange after that point in time (Figure 5).

The Great American Biotic Interchange (GABI)

Isolation ended with the formation of the Isthmus of Panama and the invasion of North American groups in South America during the Great American Biotic Interchange (GABI) in the Neogene (Carrillo et al., 2020; Cione et al., 2015a; Domingo et al., 2020; Marshall et al., 1982; Morgan, 2008; Soibelzon et al., 2019; Webb, 1976; Woodburne et al., 2006). The GABI has been considered the most important biogeographic link between South and North America by many and has been studied for a long time (Marshall, 1988; Marshall et al., 1982; Morgan, 2008; Simpson, 2005; Simpson, 1953; Stehli & Webb, 1985; Webb, 1976, 1985; Woodburne et al., 2006). More recent works have tried to offer a more reliable and better resolution by dating important layers containing the different stages of the GABI. During the GABI, North American groups moved into South America and South American groups moved into North America – however it was an asymmetric event. The majority of endemic South American groups that reached Central America became extinct (although few radiated towards North America surviving till the Pleistocene period (2.6-0.01 Ma, Prado et al. (2015)). On the contrary, most North American groups that reached South America survived and diversified. Additionally, the interchange was found to be asynchronous for mammals and plants – with floral exchanges predating the mammalian ones (Cody et al., 2010).

Marshall et al. (1982) distinguished two groups of mammalian immigrants, the first one being late Miocene immigrants that dispersed sporadically – via island arcs or non-continuous land bridge in time – as there are gaps with no arrivals at all, the number of concurrent arrivals is very limited and finally the immigrants seem to be good swimmers/floaters (Webb, 1985, 2006). However, this interpretation depends on how complete we take the fossil record of that time to be (Webb, 2006). The second group of immigrations comprised the main GABI event and was more intense than the first one (GABI 1-4; see section "GABI immigration waves").

Pre-GABI sporadic immigrations

Cione et al. (2015b) summarizes the climatic cooling taking place in South America, based on information from Tonni et al. (2008); Madden et al. (2010a). South and Central America developed drier, colder and more fragmented habitats through the Miocene and into the Pliocene (Ortiz-Jaureguizar, 1998). It also provided a variety of ecological opportunities, especially with the diverse topography of the evolved Andes (Burnham & Graham, 1999; Flynn & Swisher III, 1995). In the early Miocene, Patagonia accommodated a variety of habitats like wet forests, palm-tree habitats, flooded areas and restricted grasslands and the Andes were not blocking the wet winds from the Pacific (Madden et al., 2010). In the early Miocene, Central American habitats were tropical (Graham & Dilcher, 1998). In the middle Miocene, Patagonia went through an aridification phase – for which the formation of the Andes is considered the main driver (Pascual & Odreman-Rivas, 1973). Open habitats expanded (hosting more cursorial animals) while forests would be found in valleys of the rising Andes (hosting primates and erethizontes) (Cione et al., 2015a). The habitat and climatic changes affected some groups more than others (for example Folivora were more sensitive than Cingulata) (Cione et al., 2015a). Carrillo et al. (2015) showed an important distinction of mid and late Miocene faunas between temperate and tropical ones.

The earliest South American groups reaching North America seem to be *Pliometanastes* and *Thinobadistes* (megalonychid and mylodontid sloths) 8.5-9.0 Ma (Morgan, 2008). Additionally, the earliest record of Megatheriidae in Central America took place 5.8 Ma (Rincón et al., 2020). This seems consistent with the fact that most GABI South American groups were xenarthrans (Woodburne, 2010). The earliest North American group to South America were of the genera *Cyonasua* (procyonid carnivorans) at 7.3 Ma and sigmodontine or cricetid rodents around 6 Ma (Cione et al., 2007). Mustelids have been considered to have also entered South America by (Verzi and Montalvo, 2008) but the taxonomic classification of the fossil remains was criticised by Prevosti and Pardiñas (2009).

In the late Miocene and the boundary with the Pliocene, cooling continued, rainforests got disrupted (Lourens et al., 2004) by the extension of open environments (including savannas) and dry seasons (Cione et al., 2015a). In the Pliocene, palynological studies also show climatic cooling and further Andean uplift (Andriessen et al., 1993; Quattrocchio et al., 1988). South American xenarthran (Scillato-Yané et al., 1993) and octodontid rodent diversity shifts (Montalvo & Verzi, 2004) also showed a change in habitats that confirmed this cooling and showed that the habitat deterioration was gradual.

The next grouping of sporadic emigrations was at 5.0-4.7 Ma with *Titanis* (terror bird – otherwise endemic to South America) crossing northward (MacFadden et al., 2007) and *Plaina* and *Glossotherium* (a pampatheriid and mylodontid sloth) crossing northward to Central America (Flynn et al., 2005). The sporadic immigrations at 3.9-3.1 Ma include the northward crossing of *Glyptotherium* (glyptodont sloth), *Neochoerus* (hydrochoerid rodent) (Flynn et al., 2005) and *Pampatherium* (pampatheriid xenathran) (Woodburne et al., 2006) along with the southward crossing of Tayassuidae (artiodactyl peccaries) (Cione et al., 2007). Lastly, *Lama* (camelid artiodactyls) reached South America (Cione et al., 2007; Cione & Tonni, 1995, 2005). The timing of the first arrival of murid rodents in South America has been proposed to be late Pliocene (Marshall, 1979) but others argue for a later arrival because of the dubious stratigraphic provenance and age of the remains in question (Webb, 2006).

It is important to note that some South American groups that reached Central America dispersed further North later on: *Glossotherium* passes to the US significantly later (Flynn et al., 2005) and persists in the US for longer (McDonald & Naples, 2008). Also, *Neochoerus* reaches South Carolina at ~3 Ma (Sanders, 2002) and persisted in Florida and Arizona at least until 2.6 Ma (Bell et al., 2004; Morgan, 2005) and even more in coastal areas of North America (Morgan, 2008). These are good examples of what (Woodburne, 2010) calls “holding pen” groups, groups that occur earlier in a given location only to be significantly later in an adjacent location.

GABI immigration waves

The second group of immigrations (as distinguished by Marshall et al. (1982)) that followed comprised the main GABI event and was more intense than the first one. According to Woodburne et al. (2006), Cione et al. (2007), Woodburne (2010) and Goin, Gelfo, et al. (2012), it consisted of multiple immigration waves (GABI 1-4) during which intensified exchanges took place. Arrivals still took place during the intervals between the waves but these were significantly less frequent.

GABI 1 took place 2.6-2.4 Ma with the southward dispersal of *Erethizon* (porcupine) (Reguero et al., 2007), mustelids, perissodactyls and gomphotheriid proboscideans (López et al., 2001) and the northward dispersal of *Dasypus*, *Pachyarmatherium* (glyptodontid) and *Eremotherium* (Bell et al., 2004; Morgan, 2005) along with the “holding pen” groups *Pampatherium* and *Holmesina* (pampathere edentates) and *Neochoerus* reaching even more northern areas into the US via Mexico (Flynn et al., 2005; Morgan & Hulbert, 1995).

GABI 2 took place ~1.8 Ma and includes mostly southward dispersals of ursides, felid cats (*Felis*, *Puma*, *Panthera*), peccaries (*Catagonus*), camels, cervids, tapirs and gomphotheriid proboscideans (*Stegomastodon* and *Cuvieronius*) (Cione & Tonni, 1995, 2005; MacFadden, 2000; Pomi & Prevosti, 2005; Soibelzon et al., 2005). However, it is important to note that *Paramylodon* (Morgan, 2005) and Myrmecophaga (Morgan, 2008; Shaw & McDonald, 1987) reached the US during that interval.

In the beginning of the Pleistocene, high altitude plants are reported to have descended in lower altitudes (Andriessen et al., 1993) and precipitation is evidenced to have declined substantially (Piperno, 2006). Some also argue for a total expansion of savanna-like habitats from Central America to Argentina by the time the GABI 2 wave happened (in addition to noting the absence of tropical-adapted northward immigrants) (Webb, 1991; Woodburne, 2010). The first participation in the GABI of animals adapted to colder habitats also took place (probably because they were previously blocked by the prevalent rainforest (Webb & Perrigo, 1984). However, Colinvaux (1997) argues for the presence of sporadic rainforests in Central America during the Pleistocene. Additionally, from the Early Pleistocene, frequent glaciations are recorded in Patagonia (Singer et al., 2005) and the subsequent glacial advance (McCulloch et al., 2000) is thought to have shaped habitats to accommodate megaherbivores and their predators (Cione et al., 2015a; Tonni et al., 2003).

GABI 3 takes place at 1.0-0.8 Ma and is more of a symmetrical exchange than GABI 2. It includes the southward dispersal of carnivores and artiodactyles and the northward dispersal of the opossum *Didelphis* (Bell et al., 2004; Morgan, 2005). The modern Central American lowlands must have formed by the end of the Pleistocene and the Holocene (10.5 ka BP) (Leyden, 1984). Savanna-type habitats were not wide-spread (Behling et al., 2010) but South American coasts must have kept a savanna-type habitat similar to those in Central America (Graham & Dilcher, 1998). This has been hypothesized to have permitted the next immigration wave (Woodburne, 2010). GABI 4 takes place 0.125 Ma and is characterized by only southward dispersals of carnivores (including *Canis*, *Leopardus*) and equids (Carlini et al., 2008; Cione & Tonni, 1995, 2005; Hulbert & Pratt, 1998; Prevosti, 2006).

Post-GABI

There has been some evidence of an increased diversity in South America right after the GABI, taking into account the fossil record at face value (Cody et al., 2010; Marshall et al., 1982; Webb, 1976), and Carrillo et al. (2015) found an important increase of North American first appearances in South American faunas around 4-5 Ma with a peak in the Pleistocene. Webb (2006) calculated that diversification rates of procyonids, felids, tayassuids and camelids were moderate whereas those of canids, mustelids, cervids and murids were significantly high. North American immigrants were found to occupy a variety of South American habitats like temperate grasslands, cold winter deserts and mountain systems (Marquet & Cofre, 1999).

However, Domingo et al. (2020) found that in time, rodents, notoungulates and pilosanes switched from a C_3 to a C_4-plant dominated diet whereas litopterns and cingulates remained in a C_3 diet. This could indicate that the expansion of C_4 grasslands resulted in the presence of new niches and thus the decrease in competition (Domingo et al., 2020). On the other hand, they found gomphotheres, equids and camelids (North American groups) to show a variable diet including both C_3 and C_4 plants – an adaptation that might have helped them establish themselves in the newly found South American habitats. Finally, in carnivoran mammals, sparassodonts seemed to prefer preying on C_3 eating herbivores while carnivores preferred herbivores of a mixed C_3 – C_4 diet.

In any case, the GABI left South America changed, as the continent's faunal composition postdating the GABI resembled more that of North America than that of South American predating the GABI (Simpson, 1950; Vrba, 1992; Webb, 2006). Half of today's South America's fauna consists of North American descendants (Webb, 2006). On the other hand, diversity in North America seems to have only slightly increased after the GABI (Stigall et al., 2017). Webb (1991) comparing the diet of immigrants from Central and South American, noted that they both had grazers, browsers or mixed feeders.

Symmetricity of GABI

While the more sporadic immigrations predating 6 Ma were found to be symmetrical between continents (Bacon et al., 2015), the later and main phase of the GABI was asymmetrical, with North American groups dominating South America, compared to the low number of South American groups in North America (Bacon et al., 2015; Carrillo et al., 2020; Faurby & Svenning, 2016; Marshall et al., 1982; Webb, 2006; Webb & Marshall, 1982). This asymmetry has been a key characteristic of the GABI and has been noted from the first studies on the interchange where, e.g. Marshall et al. (1982) noted the apparent symmetrical exchange (the number of families existing before and after the GABI was very similar) but the number of North American immigrants was double that of South American immigrants.

Carrillo et al. (2020) summarized the potential causes of this phenomenon. The asymmetry could be the result of a higher dispersal rate from North to South America, higher speciation rates of North American groups in South America, higher extinction rates of South American native mammals, or equal dispersal rates but larger number of North American groups reaching South America. Testing these hypotheses, they concluded that there were no significant differences in diversification and dispersal rates of South American versus North American immigrants. However, South American native mammals in South America had significantly higher extinction rates during the GABI. This has led to fewer potential South American immigrants towards North America, and thus led to the asymmetry of the GABI.

Different theories exist that try to decipher this asymmetry. The high number of Northern immigrants to South America could have been linked to the larger area from which they originated (Webb, 1991), as well as the fact that North America was not isolated, unlike South America. North America was also linked with Europe and Asia at different points in the Cenozoic while South America was isolated, and multiple interchanges took place between Asia and North America via the Bering Strait (Tedford et al., 2004; Woodburne & Swisher III, 1995); for example, the middle Miocene arrival of gomphotherids or the late Miocene arrival of felid cats, mustelids etc. to North America. Most North American immigrants reaching South America had previous evolutionary records of long-distance dispersals and this could have been linked to their GABI success (Webb, 2006). They were also more "evolutionary tested" coming into contact with various competitors, diseases (Wilson, 1992), and habitats, especially savannas and temperate areas (Jetz & Fine, 2012). These would potentially increase their capability to colonize new locations and occupy new niches there (Wilson, 1992).

There are different hypotheses concerning the high extinction rates of South American native mammals in South America. One was that the extinction was linked with increased competition, as SANU diversity decline coincides with the appearance of the numerous North American ungulate immigrants (artiodactyles mostly) (Webb, 2006), and thus a replacement phenomenon could be implied (Webb, 1976). However, raw taxon counts have shown that meridiungulates and marsupial carnivores had already started to decline before the GABI (Kemp, 2005). SANU's decline could have been intensified due to competition with artiodactlyles (Webb, 1976) or due to higher susceptibility to predation from placental carnivores (Faurby & Svenning, 2016; Patterson & Pascual, 1968), that surpassed marsupial carnivores (sparrassodonts) in numbers (Prevosti & Forasiepi, 2018).

Another hypothesis was that the extinction was triggered by environmental change towards a colder and drier climate (Alberdi et al., 1995), as described in previous sections of this thesis. Carrillo et al. (2020) also note that most of the South American native mammal diversity at the time comes from the La Pampas formation, where a meteoric impact has been evidenced ~3.3 Ma (Schultz et al., 1998; Vizcaíno et al., 2004). Finally, another theory suggests a synergetic effect of environmental changes, ecological opportunism and biotic interactions (Marshall, 1988; Stehli & Webb, 1985; Vrba, 1992, 1993; Webb, 1991, 2006).

Selectivity of the GABI

Different hypotheses have been made on the nature of the timing and selectivity of the immigrations. It has been noted that most animals crossing have been assumed to have been savanna-adapted (Stehli & Webb, 1985; Webb, 1985, 1991, 2006; Woodburne, 2010) and that the Panama habitats were also savanna-like (Piperno, 2006; Piperno & Jones, 2003) and some have implied that habitat preference played a key role (Stehli & Webb, 1985; Webb, 1985, 1991, 2006).

Additionally, McDonald (2005) and McDonald & Naples (2008) noted a diet-linked advantage in xenarthrans: glyptodont immigrants reaching Central/North America were smaller, generalists and their diet was comparable to that of non-ruminant artiodactyls (signalled by the absence of a caecum) and so liberated them from competition with the ruminant artiodactyls and proboscideans. According to these studies, this was also heightened by the lower metabolic rate of xenarthrans. All this potentially played a key role in the high participation of xenarthrans in the GABI as well as in their colonisation of Central and North American habitats.

Multiple studies have also argued that the climate cooling played a key role in the initiation and regulation of the interchange (Cione et al., 2015a; Marshall, 1985; Marshall et al., 1979, 1982; Molnar, 2008; Webb, 1978, 1985, 1991, 2006; Woodburne, 2010) by rendering regions suitable for animals to cross (thus working as corridors) or unsuitable (biogeographic barriers) (Webb, 1991; Woodburne, 2010). Sea level might have also played an important role in the dispersion control as the low sea levels at 2.5, 1.9, 1.6, 0.7, 0.1 Ma seem to coincide with the dispersals (Woodburne, 2010).

The evolution of the Panama isthmus (presence or absence of a continuous strip of land etc.) must have played a key role as well, however, other variables must have played a more important role controlling the directions, timing and speed of the interchanges (Jaramillo, 2017). The evolution of the Andes (extending N-S long in SA; see also dedicated section) (Boschman, 2021; Ramos, 1999)) has been suggested as another factor controlling dispersals within South America, as they reached today’s elevations during or soon after the late Miocene (Mora et al., 2010) and may have constituted a colonization corridor during the GABI (Patterson et al. (2012) and refs therein).

There is still no consensus, and of course, more than one factor is expected to have driven the GABI and the diversity shifts. However, Bacon et al., 2015) found that taxa variability and dispersal time were not explained by intrinsic factors (like dispersal ability, biome and elevation preference). Additionally, Bacon et al. (2016) specify that within the potential extrinsic factors, climatic and environmental factors were key while geologic factors did not play a significant role. Vrba (1992) also noted the importance of environmental changes over biotic interactions as the major cause of biotic event.

Preservation issues

The issue with the majority of GABI studies, hypotheses and interpretations is that they heavily rely on raw diversity counts. This means that fossil biases could actually have an enormous effect on raw diversity and so make those interpretations invalid. This has been brought to attention from the early studies like Marshall et al. (1982) that pointed out that the late Cenozoic South American mammalian record mostly comes from Argentina – but it is safe to assume that what took place there must have taken place in the rest of South America. Webb (2006) also mentioned the “Central America paradox”: it refers to the fact that while Miocene Central America faunas showed no similarity with South American faunas (Ferrusquía-Villafranca, 2003; Webb & Perrigo, 1984), today’s faunas and floras are similar to those of South America. This is coupled with a lack of intermediate fossils. This is of course, a fossil record bias, especially concerning Pliocene and Pleistocene fossils from Central America. (Goin, et al., 2012a) stated that the radiations and distribution patterns of South American mammals “offer a narrative framework for considering the mammalian successions in South America, hoping that future tests of [their] model will confirm, clarify, and extend its applicability, causes, and consequences”. These kinds of quantitative studies exist (e.g. Bacon et al. (2015)) but are still scarce. One such example is Carrillo et al. (2020), using a large dataset and advanced statistical techniques, such as Bayesian methods, to take into consideration fossil bias. Carrillo et al. (2015) also tried to bypass the issue of uneven sampling between high and low altitudes when looking at the similarity between different faunal assemblages, but still states that fossil biases could impact their results.

The effect of the Andean orogeny on South American climate and habitats

Due to their complexity, mountains generally provide a broad range of habitats, and are thus linked with high diversity (Badgley et al., 2017; Hoorn et al., 2018; Perrigo et al., 2020). They can work as cradles, nursing a diversity of taxa in these “endemic” micro-habitats (Hughes & Atchison, 2015), as bridges or barriers of taxon dispersal, as well as refuges for taxon diversity (Perrigo et al., 2020). Mountains influence climate as well as close and distant habitats, being the start point of river systems, and sediment generation and transportation (Finarelli & Badgley, 2010; Hoorn et al., 2018; Hoorn, Wesselingh, Hovikoski, et al., 2010).

Today, the Andes Mountains are one of the globe’s biodiversity hotspots, hosting the highest number of vertebrate and plant species (Myers et al., 2000), and its evolution is thought to have played an important role in this richness (Antonelli et al., 2018; Boschman & Condamine, 2022; Hoorn, Wesselingh, ter Steege, et al., 2010; Pérez-Escobar et al., 2022), as well as in transforming the South American continental habitats and climate, working in tandem with the already existing global climate cooling.

The evolution of South American climate and habitats started to diverge from the global palaeoclimatic and palaeoenvironmental trend, because of the formation of the Andes. The evolution of the Andes has been the most (or one of the most) important factor driving the evolution of the Amazonian habitats and ecosystems via its direct impact on the topographic evolution but also indirectly via its influence on the local climate (Hoorn, Wesselingh, ter Steege, et al., 2010). More specifically, intense tectonic changes –

specific to South America – took place in the end Cretaceous and first half of the Cenozoic that resulted in extensive tectonic pressure and subsequent deformation of the Northern and Central regions of South America (Pan-Amazonia) – including the formation of the Andes (Hoorn, Wesselingh, ter Steege, et al., 2010; Isacks, 1988). Andean uplift has been diachronous ever since (Boschman, 2021; Figure 5D), as the mountain range's different parts have been subject to different tectonic forces (Gianni et al., 2018; Pérez-Escobar et al., 2022; Schepers et al., 2017).

The end Cretaceous and Paleogene was characterised by relatively low Andean uplift rates, which primarily occurred in the central and northern parts of the mountain range (Boschman, 2021; Boschman & Condamine, 2022). The Cretaceous Pan-Amazonia hosted vast river and lake systems of which a substantial number of rivers had a westward flow (opposite to what exists today) (Mapes, 2009). These shifted to low altitude regions (Hoorn, Wesselingh, ter Steege, et al., 2010), having a mix of marginal marine embayments (Roddaz et al., 2010) and drainage systems flowing both eastward and westward (Figueiredo et al., 2009) during the first half of the Cenozoic. At the end of the Paleogene, drainage systems changed (Sena Costa et al., 2000) with the direction of flow towards the northwest (Hoorn, Wesselingh, ter Steege, et al., 2010), while dense forests started getting replaced by open shrublands (Dunn et al., 2015).

An intensification of Andean uplift took place in the Neogene, with mountain building taking place mainly in Northern and most notably East-Central Andes (Boschman, 2021; Boschman & Condamine, 2022; Tournier et al., 2020). More specifically, Andean uplift showed a peak in the early Miocene ~23 Ma (Hoorn, Wesselingh, ter Steege, et al., 2010), but its most intense mountain building events took place in the late middle Miocene ~12 Ma and Pliocene 4.5 Ma (Mora et al., 2010).

In the regions of the Pan-Amazonia, the environment shifted to a complex of vast shallow lakes and swamps around 23-10 Ma (Hoorn, Wesselingh, ter Steege, et al., 2010). These disappeared and fluvial systems took their place (Hoorn, Wesselingh, Hovikoski, et al., 2010; Hovikoski et al., 2007; Latrubesse et al., 2010), starting resembling its present form (Mora et al., 2010). River flow shifted from westward to eastward permanently ~7 Ma and that is when the Amazon drainage system got fully established (and is unchanged till today) (Figueiredo et al., 2009). Additionally, to the topography-related changes, the evolution of the Andes influenced the South American climate (Insel et al., 2010; Poulsen et al., 2010).

With the extensive mountain uplifting, the Andes formed a barrier that extended from the continent’s highest to lowest altitudes. This prevented Pacific humid winds from reaching the central and eastern parts of the mountain chain, thus promoting aridification in those regions (in conjunction with the ongoing global aridification and cooling), while increasing precipitation in the western side of the mountain range (Cione et al., 2015b; Figueiredo et al., 2010; Hoorn, Wesselingh, ter Steege, et al., 2010; Insel et al., 2010; Ortiz-Jaureguizar & Cladera, 2006; Pascual & Odreman-Rivas, 1973; Poulsen et al., 2010; Quattrocchio et al., 2003; Rech et al., 2006).

The Latitudinal Biodiversity Gradient (LBG)

Most groups of South American mammals are characterized by a latitudinal biodiversity gradient (LBG) today, as are most extant groups. The LBG is the fundamental macroecological pattern that describes the distribution of diversity today and it refers to the increase of the number of species towards the equator (Fergnani and Ruggiero, 2015; Kaufman, 1995; Stevens et al., 2019; this thesis [Supplementary material or SI section 14]; Figure 6).

Understanding what drives this global, first-order pattern remains one of the great challenges of macroecology (Pontarp et al., 2019). Mittelbach et al. (2007) reviewed the two main hypotheses for the origin of the LBG: (1) the time and area hypothesis according to which tropical habitats are older and taxa accumulated there over a longer period compared to higher latitudes and (2) the diversification rate hypothesis according to which taxa in tropical regions diversify faster. They concluded that a greater amount of evidence (both palaeontological and modern) supports the diversification rate hypothesis (Jablonski et al., 2006; Mittelbach et al., 2007; Schumm et al., 2019; Wiens & Donoghue, 2004). In other words, lower diversity in higher latitudes would be the result of lower diversification rates. Dispersal must have also played a role in shaping the LBG pattern, and climatic factors have been key drivers of diversification and dispersal rates (Meseguer & Condamine, 2020).

The interplay of mechanisms behind this diversification differences between high and low latitudes are not yet clear (Arita & Vázquez-Domínguez, 2008): three possible patterns were summarised in Arita and Vázquez-Domínguez (2008):

- The “tropics as cradle” model in which origination rates increase towards the tropics while extinction rates remain constant with latitude (Chown & Gaston, 2000; Krug et al., 2009; Mittelbach et al., 2007)
- The “tropics as museums” model in which origination rates remain constant with latitude but extinction rates decrease towards the tropics (Chown & Gaston, 2000; Krug et al., 2009; Mittelbach et al., 2007; Weir & Schluter, 2007)
- The “out of the tropics” model in which origination rates increase and extinction rates decrease towards the tropics and dispersal from low to high latitudes plays an important role (Jablonski et al., 2006, 2013)

Multiple studies have found higher speciation rates towards the tropics (Allen et al., 2006; Allen & Gillooly, 2006; Jablonski, 2008; Jablonski et al., 2006; Kiessling et al., 2010; Krug et al., 2009; Krug, Jablonski, et al., 2007; Krug, Patzkowsky, et al., 2007; McKenna & Farrell, 2006) and, more recently, Saupe, Myers, et al. (2019) concluded that high tropical diversity resulted primarily from higher speciation, and that dispersal towards higher latitudes was important, thus supporting the “out of the tropics” hypothesis.

However, aspects of these models have been questioned. For example, Weir and Schluter (2007) found that origination and extinction rates decrease towards the tropics, and Krug et al. (2010) found higher extinction rates towards the poles. Wiens et al. (2006), Mittelbach et al. (2007), Arita and Vázquez-Domínguez (2008), Soria-Carrasco and Castresana (2012), among others, found no change in diversification rates by latitude. Rabosky et al. (2018) showed a higher speciation rate of fish in higher latitudes. Pontarp et al. (2019) stated that this large number of studies, hypotheses and conflicting results comes from the failure to link ecological and evolutionary processes with the LBG.

Other studies have tried to explore different aspects of the LBG. Kinlock et al. (2018) showed that the present-day LBG is stronger in the western hemisphere, Silvestro, Castiglione, et al. (2019) found that extinction rate decreases with species age and this age-dependent extinction pattern is stronger towards the Equator. Schumm et al. (2019) showed that tropical faunas have higher functional richness but lower functional evenness than temperate faunas. Castro-Insua et al. (2018) observed a link between species range shape and latitude.

The present-day LBG pattern did not always exist (Mannion et al. (2014) and references therein). Equator-to-pole diversity gradients have been observed during the Palaeozoic era (Alroy et al., 2008; Jablonski et al., 2013; Krug, Patzkowsky, et al., 2007) as well as in the last ~30 Myr (Marcot et al., 2016; Yasuhara et al., 2012). Mannion et al. (2014) pointed out that the presence of a LBG coincided with periods where the Earth presented permanent ice sheets at both poles (icehouse intervals). On the other hand, instances of flat or temperate-peak LBGs (Archibald et al., 2010; Kiessling et al., 2012; Mannion et al., 2012; Rose et al., 2011; Smith et al., 2012; Yasuhara et al., 2012) seem to exist during warm periods like greenhouse intervals or interglacial periods (Mannion et al. (2014); Jones et al. (2019); but see also Kiessling et al. (2012) for a different view). Climate change was found to drive the LBG patterns through time (Meseguer & Condamine, 2020).

The evolution and causes of the present-day LBG have been the focus of multiple studies; nevertheless, it is a phenomenon that remains poorly understood – and like other similar diversity patterns of the past, it is important to take into account the fact that they can be obscured by geological and human-related biases (Benson & Upchurch, 2013; Smith & McGowan, 2007; Upchurch et al., 2011). Some studies suggest the modern-LBG first appeared around 30 Ma (Mannion et al. (2014) and references therein). On the other hand, based on their study on North American mammals, Marcot et al., 2016), suggested that this was formed only 4 Ma. The understanding of the formation and causes of the present-day LBG is essential in comprehending the link between climate and biodiversity, as well as predicting how biodiversity will respond to future global warming. The appearance of the present-day LBG has not been extensively explored in South America either. Consequently, the relative roles of climate, Andean uplift, and the GABI on shaping South America's LBG have never been tested, but could illuminate our understanding of its emergence.

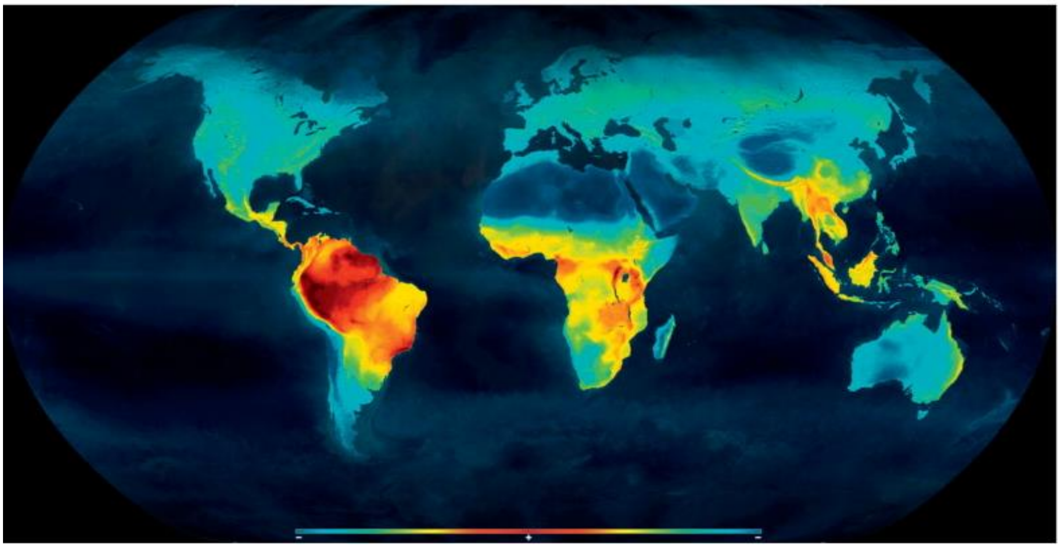

Figure 6: The present-day distribution of terrestrial vertebrate diversity follows the present-day Latitudinal Biodiversity Gradient, figure from Mannion et al. (2014). Red indicates higher diversity and blue hues indicate lower diversity.

Fossil record bias

The fossil record is valuable for understanding the past – it is however biased and the biological signal we want to study gets distorted (Allison & Briggs, 1993; Alroy et al., 2008; Forey et al., 2004; Peters & Foote, 2001; Raup, 1972, 1976; Sepkoski et al., 1981; Smith & McGowan, 2007, 2011). Past biological signals (e.g. diversity or diversification rate shifts) get obscured/distorted through the taphonomical/geological processes but also sampling effort (Alroy et al., 2001; Benton, 2008b, 2008a; Forey et al., 2004; Marx & Uhen, 2010; Peters, 2005; Peters & Foote, 2001; Raup, 1972, 1976; Smith, 2001; Smith & Benson, 2013; Smith & McGowan, 2011; Tarver et al., 2011; Uhen & Pyenson, 2007) (Figure 7).

Taphonomical/geological biases refer to the fact that not everything that dies becomes a fossil and survives the tectonic and geological processes until the present day (Figure 7). This can be due to the organism’s composition (organisms with hard parts like bone get fossilized substantially more), its living habitat (some habitats have higher preservation capability than others like lakes with still water and high sediment flux), the geological processes acting on the area (extreme deformation or metamorphism can destroy fossils) and its subsequent position today (due to tectonism fossiliferous rocks can end up in the surface thus getting exposed to erosion or in big depths thus being inaccessible).

Sampling biases refer to the fact that not everything that becomes a fossil gets discovered, studied and published (Figure 7). There is a significant variation in sampling effort depending on the cultural and economic situation of each country or region (the presence of universities and museum institutions etc.) with an extreme high in the US. Finally, there is a significant variation in sampling effort depending on the organism group, with some groups (e.g. dinosaurs) being very popular and thus more intensely sampled and less popular groups like invertebrates or plants being undersampled.

For example, numerous studies have found correlations between observed (= ”raw”) vertebrate diversity and sampling (Barrett et al., 2009; Benson et al., 2016; Butler et al., 2011; Cleary et al., 2018; Close et al., 2020a; Close et al., 2017; Dunne et al., 2018). Peters and Foote (2001) found that variation of marine diversity is an artefact of variation in rock availability and Kalmar and Currie (2010) showed that the marine record is far more complete than the terrestrial one. The early tetrapod fossil record is represented by few localities, the distribution of which is totally different between time periods, according to Benton (2015). Additionally, Tennant et al. (2018) showed that our understanding of dinosaur evolution changed throughout historical time, while Hunter and Donovan (2005) and Forcino and Stafford (2020) noted the presence of biases in the way palaeontologists collect/sample fossils. Finally, Riddle and Jezkova (2019) mentioned that within Mammalia, there is a publication bias towards papers on rodents.

Older studies evaluated the fossil record at face value, like for example Sepkoski et al. (1981), Benton (1995) and Sepkoski (1997). The issue of fossil biases first was first evaluated 50 years ago, with Raup (1972, 1976) arguing that taxonomic diversity fluctuations follow sedimentary fluctuations or sampling effort. Koch (1978) mentioned a bias in the published fossil record. Raup (1972, 1979) introduced the “Pull of the Recent” effect; he originally described this as the phenomenon according to which the better sampling of extant taxa results in the extension of the stratigraphic ranges of their most close fossil relatives to the present. On the contrary, this cannot be done for older taxa, therefore this can lead to an artificial diversity increase towards the present. However, this effect has mostly been used as a more general term to describe the increase of raw diversity towards recent time intervals because of the higher potential of sampling fossils in these more recent beds. Pease (1985) tried to amend this issue by introducing the “duration truncation” mechanism. Benton et al. (2000) showed that fewer fossils are found in older rocks and proposed that a temporal and taxonomic scaling is applied in order to uniform the documentation of life in the past. Signor and Lipps (1982) pointed out that because the fossil record is biased, it is unlikely that the first and last appearances of fossil species represent the true first and last appearances of the group in reality, a fact that complicates studying mass extinctions for example (the Signor-Lipps effect).

Early studies have tried to take into account and amend for fossil biases by looking at the relation of sediment and taxonomic fluctuation (Allison & Briggs, 1993; Sepkoski et al., 1981) or predicting the true diversity (Foote & Sepkoski, 1999). Later, a variety of methods has been developed in order to reconstruct the real biological signal accounting for fossil biases. Those include the use of sampling proxies, completeness metrics as proxies and subsampling methods.

The use of sampling proxies consists of the correction of fossil bias with the use of proxies like fossil-bearing formation or collection counts or a residual method described by Smith and McGowan (2007). Various studies have used that (Barrett et al., 2009; Butler et al., 2013; Mannion et al., 2011; Smith & McGowan, 2007). In the regional scale of New Zealand, Crampton et al. (2003) found that outcrop area seems a reliable proxy for rock volume – but not formation count. However, Dunhill et al. (2012, 2014) argues that sampling proxies only partially represent fossil biases and should thus be avoided.

Another way studies have tried to take into account fossil bias is with the use of completeness metrics as proxies for preservation bias (Beardmore et al., 2012; Beardmore & Furrer, 2016; Brocklehurst et al., 2012; Brocklehurst & Fröbisch, 2014; Cleary et al., 2015; Dean et al., 2016; Mannion & Upchurch, 2010). There is a causal link between completeness metrics and diversity as more complete specimens are needed in order for a taxonomic identification to happen (Benton et al., 2013). On the other hand, Mannion and Upchurch (2010) argue that completeness metrics should not be used as bias proxies and the study of Cleary et al. (2015) also support that view.

Finally, the use of subsampling methods has been more recently used to estimate diversity through time taking into account fossil biases (Alroy, 2010b; Benson et al., 2016; Brusatte et al., 2015; Mannion et al., 2012, 2015; Nicholson et al., 2015). Two main subsampling methods have been used in the literature. The earlier one has been Classic Rarefaction (CR) (Miller & Foote, 1996; Raup, 1975) according to which random samples of individuals (individual-based) or groups of individuals (sample-based) are drawn for the whole occurrence dataset in order to generate an expected taxa count according to sampling intensity level CR and multiple studies have used that (Alroy et al., 2001, 2008; Fastovsky et al., 2004; Mannion et al., 2011; Raup, 1972, 1979). Later, a more sophisticated sample-standardising method came out by Alroy (2010b), called Shareholder Quorum Subsampling (SQS) and this is the primary method that is going to be used to estimate past diversity in this thesis.

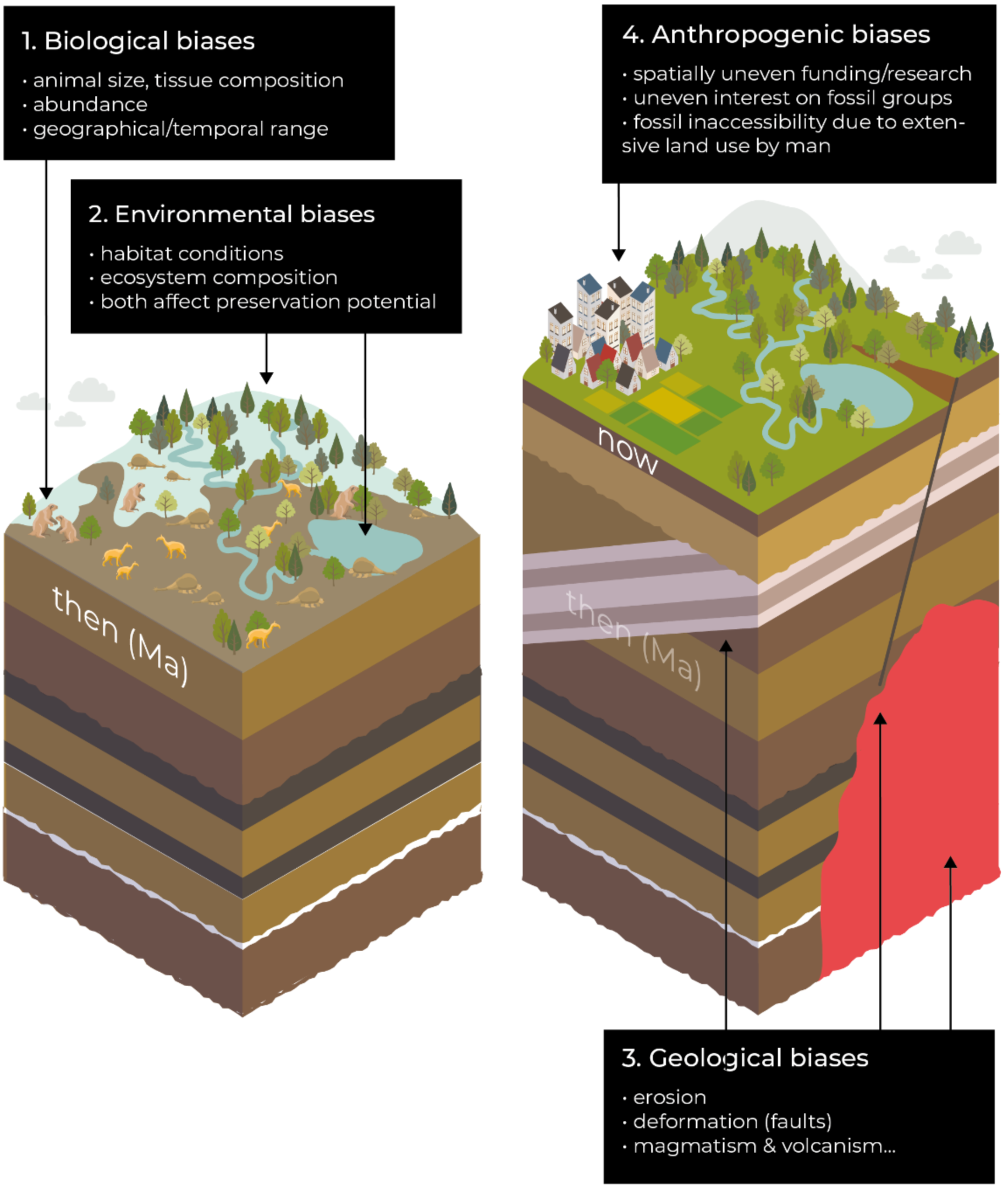

Figure 7: Schematic presentation of the different types of fossil biases. Biological biases refer to the difference preservation potential due to animal size and tissue composition (those with ossified parts fossilize substantially better), abundance and geographical/temporal range (those with a large abundance and range have more probability of getting fossilised). Environmental biases are due to environments and ecosystems having different preservation potential. Geological biases come from the long processes of the Earth like sediment/rock deformation (faulting, folding etc.), magmatism and metamorphism (that destroy fossils) and erosion of the rocks and fossils that come out on the surface. Finally, anthropogenic biases refer to the spatially uneven potential of fossil discovery and research (because of the uneven spatial distribution of funding and/or expertise), the favouritism towards some fossil groups (like dinosaurs) and the inaccessibility of an important part of the Earth's surface because it is occupied for other uses. Biological and environmental processes are "quick" (taking from days to decades at a point in time in the past) compared to geological processes (taking Myrs).

Aims of this thesis

Despite South America's present-day biodiversity emergency and exceptional geobiological history, our knowledge of the continent's faunal evolution is still in its infancy, limiting our understanding of how the present-day distribution of biodiversity was assembled. Major knowledge gaps still exist, including the impact of geologically long-term climatic change on the continent's mammals, and the appearance of the present-day LBG on the continent. In this thesis, I evaluate spatiotemporal fluctuations in diversity and diversification dynamics of South American terrestrial eutherian mammals during the Cenozoic (66 to 0.012 Ma) including testing the potential roles of palaeoclimatic, palaeoenvironmental and tectonic drivers in shaping these patterns. I apply a novel combination of quantitative methods that accounts for uneven temporal and spatial sampling to a near-comprehensive fossil occurrence dataset from the Paleobiology Database, and utilise model-induced palaeoenvironmental data local to South America. I compare these results to biodiversity patterns of metatherian mammal and other terrestrial vertebrate groups present on the continent. Finally, I evaluate the probable causes and timing of the emergence of the present-day terrestrial LBG in South America.

Material and Methods

Occurrence dataset

An important part of my work consisted of data entering in the Paleobiology Database (PBDB). This is an online, collaborative and open database storing fossil occurrences and information on their taxonomy, as well as stratigraphical and geographical position; paleocoordinates of fossil occurrences (along with position, size and form of the continents in the past) are sourced from Paleomap Project by Christopher R. Scotese (http://www.scotese.com) – paleogeographic rotation models. PBDB enterers first add a “reference” (i.e. a publication such as a scientific paper, book section, etc.) and from there they extract information on the taxonomy of the fossils mentioned (i.e. “authority” data and “opinion” data) as well as on the “collection” (i.e. the locality the fossil(s) were found, like age, geology and stratigraphy). This is where the occurrence(s) are added afterwards. It is not a quick process, but it ensures that all the information get stored in a concise way and that they are more easily accessible to more researchers.

I compiled an occurrence dataset of Cenozoic South American terrestrial mammals in the Paleobiology Database (PBDB; https://paleobiodb.org/), having entered 1654 new fossil occurrences from 450 collections and 168 references (that is ~25% of the dataset used in this thesis). In addition, I manually checked the validity of all existing occurrences in the PBDB, and where necessary, I updated their taxonomy and stratigraphy based on the latest literature. To detect possible spatiotemporal occurrence errors, I used the CoordinateCleaner R package ver. 2.0.2 (Zizka et al., 2019). This identified 246 possible outliers (0.04% of the total occurrences), which I evaluated and corrected where necessary. Following these additions and revisions, the PBDB includes a spatiotemporally and taxonomically up-to-date representation of the published literature on Cenozoic South American terrestrial mammals, as of the 3rd February 2021.

For my analyses, I downloaded all South American mammal occurrences from the PBDB on the 21st March 2021, with non-body fossils (e.g. trace fossils), marine and volant species (i.e. Chiroptera) excluded. Collections identified in the PBDB as having a poor spatial resolution (i.e. local area and basin-level) were also excluded as such data lack specific geographic coordinates. Similarly, temporally unconstrained occurrences with an age range greater than the largest time bin in my thesis (i.e. the Ypresian, spanning 8.2 Myr) were also excluded. The final dataset comprises 6463 fossil occurrences of South American terrestrial eutherian mammals, representing 1325 genera and 1630 species, as well as 804 fossil occurrences of South American metatherians, representing 244 genera and 281 species.

Collection stratigraphic ages and time binning

A large proportion of the fossil occurrences in the PBDB are assigned to South American Land Mammal Ages (SALMA), some of which are currently out-of-date in the PBDB. Therefore, following the dataset download and before assigning time bins, I updated the SALMA' maximum and minimum age limits for each collection according to the latest published literature (see SI section 1).

To account for the age uncertainty of the fossil occurrences and the discord between SALMA and international chronostratigraphic stages (see SI section 1), I generated random absolute ages for each fossil collection by sampling a uniform distribution, defined by the collection's maximum and minimum age range. Using these generated ages, I subsequently binned occurrences into my time bins. This process was repeated 100 times (i.e. 100 occurrence datasets were generated), using the extract.ages() R function from pyrate_utilities.r (Silvestro et al., 2014).

To test the sensitivity of my results to the time binning protocol, I performed preliminary analyses with three different schemes, in the first year of this project, but no notable differences to the overall results were found, and herein I present results from stage-level analyses, which maximise the amount of stratigraphically resolved data. Because of their short duration, I combined stages of the Pleistocene (2.588–0.012 Ma) into a single time bin.

Latitudinal binning

For the latitudinal analyses, I binned occurrences into 15° latitudinal bins, following several other palaeobiological studies (Jones et al., 2021; Kröger, 2017; Mannion et al., 2012; Nicholson et al., 2016). During preliminary analyses, 10º latitudinal bins were also considered, however, they proved too fine scale to provide meaningful results, with insufficient sample sizes in each bin. Occurrences were temporally binned into the following time bins: Paleocene (66–56 Ma), Eocene (56–33.9 Ma), Oligocene (33.9–23.03 Ma), early (23.03–15.97 Ma), middle (15.97–11.63 Ma) and late Miocene (11.63–5.33 Ma), Pliocene (5.33–2.58 Ma), and Pleistocene (2.58–0.01 Ma). Preliminary analyses were also conducted at stage level; however, limited data availability prevented the production of meaningful results (SI section 12). Although some of the chosen temporal bins are of long duration, they capture substantial shifts in the Earth's climate system, tracking the transition from greenhouse to icehouse conditions (Inglis et al., 2015; Thomas, 2008; Zhang et al., 2019).

To compare past eutherian latitudinal diversity trends with those of extant members of the clade, I downloaded placental mammal occurrences from the Global Biodiversity Information Facility database (gbif.org; dataset DOI: 10.15468/dl.sex4w9), removing marine and volant species, as well as any occurrences representing fossil remains. I then binned these extant occurrences into 15° latitudinal bins and calculated counts of families, genera, species, and localities (SI section 14).

Palaeoenvironmental and topographic datasets

Stage-level climate and topography simulations for the Cenozoic were carried out using the HadCM3BL-M2.1aD model, a version of the Bristol HadCM3BL coupled atmosphere-ocean general circulation model (Valdes et al., 2017). The HadCM3L model used here has a horizontal resolution of 2.5° x 3.75° in the atmosphere and ocean, with a vertical resolution of 19 levels in the atmospheric component, and 20 levels (5550 m depth) in the oceanic component (Valdes et al., 2017). HadCM3BL has been shown to perform well in reproducing average global and regional scale climate patterns recorded in proxy data (Farnsworth, Lunt, O'Brien, et al., 2019; Saupe, Farnsworth, et al., 2019; Sellwood and Valdes, 2006; Valdes et al., 2017), and has recently been used in a number of palaeobiological studies (e.g. Chiarenza et al. (2019); Dunne et al. (2020); Saupe, Farnsworth, et al. (2019); Waterson et al. (2016)). For the stage-level climate simulations, the CO_2 concentration was held constant at 1,120 ppmv for the Paleogene and Eocene, 560 ppmv for the Oligocene, and 400 ppmv for the Neogene and Pleistocene. Model boundary conditions (topography, bathymetry, and ice sheet configurations; at 0.5 x 0.5° resolution and downscaled to model resolution) for each geologic stage following the methods of Lunt et al. (2016). Stage-specific solar luminosity was calculated using the methods of (Lunt et al., 1981).

Each palaeoclimatic simulation was initialised from a set of stage-level simulations from Farnsworth, Lunt, O'Brien, et al. (2019) that was already spun-up for 10,422 years. A new implementation of the ozone scheme in HadCM3BL was adopted that dynamically identifies the height of the tropopause whose height can increase higher into the troposphere in warmer climates such as those during the Paleogene. The new scheme also makes sure that stratospheric ozone cannot penetrate into the troposphere, which would be unphysical. The 3-D ozone distribution scheme was therefore replaced by the Meteorological team in Bristol with a simple dynamic one in which ozone is coupled to the model's tropopause height and use constant values for the troposphere (0.02 ppm), tropopause (0.2 ppm), and stratosphere (5.5 ppm). This change makes a negligible difference to the global mean surface temperature but does have a small impact on the stratospheric temperature (~-6 °C in the pre-industrial simulation) and winds (~-8 m/s for the pre-industrial). These simulations were run by the team for a further 6,000 years to ensure full surface and deep ocean equilibrium. Experience has shown it can take many thousands of model years (sometimes upwards of 10^4 years to fully equilibrate to all of the model boundary conditions, particularly in the deep ocean. This is essential so that model atmosphere and ocean circulation is representative of stage-level boundary conditions.

From the palaeoclimatic simulations, I extracted near-surface (1.5 m above ground) mean annual temperature and precipitation for the South American continent. Using these data, I calculated the mean, minimum, and maximum values of temperature and precipitation for each stage-level bin, and each latitudinal bin (15°). Stage-level topographic data for the South American continent were extracted from Getech's digital elevation models (DEMs), which provide gridded (0.5° x 0.5°) representations of the Earth's topography and bathymetry. These DEMs serve as the boundary conditions for the climate simulations (Markwick, 2019; Markwick & Valdes, 2004), and provide explicit data for when the configuration of the continents were different from today. These models have been used in a number of recent deep-time climate niche studies (Dean et al., 2019; Jones et al., 2021; Lyster et al., 2020; Saupe et al., 2020).

I also extracted global palaeotemperature proxies from Westerhold et al. (2020), which is based on global $\delta^{18}O$ isotope reconstructions from benthic foraminifera. I used the mean of these values for each of my time bins. Lastly, data on Andean topography were extracted from Boschman (2021) and Boschman and Condamine (2022). These are estimates of palaeoelevation of the Andean region throughout the last 88 Myr. I used the mean of these values for each of my time bins. The Andean uplift was diachronous, with different regions of the Andes having different pulses of uplift during the Cenozoic (Boschman, 2021). Although the use of mean Andean uplift does not allow us to evaluate regional variation in the influence of Andean uplift on diversification of eutherian mammals, it is a useful proxy to evaluate the relationships between orogeny, fossil sampling, and eutherian mammal diversification at a continental scale, which is the focus of this thesis.

Raw taxonomic counts, sampling, and alpha diversity

Given that genus-level analyses enable the inclusion of a greater amount of data (i.e. specifically indeterminate remains can be retained), and that fossil species identification is more prone to taxonomic bias, I restrict most of my analyses to genus-level (see alpha diversity below for an exception). Furthermore, a Spearman's correlation test showed a statistically significant, strong positive correlation between mean counts of genera and species (Rho = 0.931; $p < 0.001$).

For each time bin, I calculated the mean of counts of sampling proxies (collections, formations, occupied equal area grid cells, and reference counts) from dataset replicates ($n = 100$). Occupied equal-area grid cells were generated using the dggridR R package ver. 2.0.4 (Barnes & Sahr, 2017), with 100 km spacings. To evaluate the influence of sampling on observed diversity trends, I calculated the Spearman's correlation coefficient between mean counts of each sampling proxy and mean counts of genera.

I estimated alpha diversity (local richness) by counting the number of eutherian mammal species per fossil locality (= PBDB fossil collection, which is a specific geographic point and stratigraphic level). To compliment these estimates, I also calculated 'cryptic' diversity by including specifically indeterminate occurrences in each collection that potentially represent additionally distinct species. Despite its potential to be informative, and enabling the inclusion of a greater amount of fossil data, cryptic diversity has been largely overlooked in palaeobiodiversity analyses, with few exceptions (Close et al., 2019; Dunne et al., 2018; Mannion et al., 2011).

I calculated cryptic alpha diversity using two methods, which I refer to as the 'relaxed' and the 'conservative' approach. The 'relaxed' approach is comparable to recent work, in which it was termed 'indeterminate richness' (Close et al., 2019; Dunne et al., 2018). Under this approach, alpha diversity equals the number of unique occurrence names in any given collection, with all specifically indeterminate occurrences (e.g. Genus sp. or Family indet.) counted as distinct species. The second method, the more 'conservative' approach, is analogous to that applied by Mannion et al. (2011). Under this protocol, specifically indeterminate occurrences are considered distinct only if they belong to a higher taxonomic level (e.g. order) not already represented in the collection. This is best illustrated with an example of a hypothetical fossil locality that contains the following four occurrences: Macrauchenidae indet., Toxodontia indet., *Macrauchenia patagonica,* and

Macrauchenia sp. (SI section 2). Alpha diversity, calculated in the standard approach, for that locality would be equal to one, as the only recognised species for this collection would be *Macrauchenia patagonica*. However, under the conservative protocol, cryptic alpha diversity for the same collection would equal two, with the recognition of the additional distinct species, Toxodontia indet. Finally, under the relaxed protocol, cryptic alpha diversity would equal four, with *Macrauchenia* sp. and Macrauchenidae indet. also recognised as distinct species. To evaluate whether these two measures of cryptic alpha diversity scale with standard alpha diversity, I carried out Spearman’s rank correlation coefficient tests.

Sampling-corrected diversity and diversification rates

To calculate diversity, as well as rates of speciation and extinction through time and space, accounting for sampling biases, I used two methods with different computational approaches: coverage-based rarefaction and PyRate. Plots of my results were produced with the ggplot2 R package ver.3.3.5 (Wickham, 2016), and the geological timescale was added with the deeptime R package ver. 0.2.2 (Gearty, 2020).

Coverage-based rarefaction

Coverage-based rarefaction (Chao & Jost, 2012), or Shareholder Quorum Subsampling (SQS) as it is more commonly known amongst palaeobiologists (Alroy, 2010a), is a widely applied subsampling approach used to account for uneven sampling in the fossil record (e.g., Close et al., 2020a; Close et al., 2018; Dunne et al., 2018). SQS calculates diversity between bins in an objective, frequency-dependant way that is not driven by sampling (Chao & Jost, 2012). For each bin, it calculates taxon frequencies, i.e. the proportion of occurrences of each taxon relative to the total (Alroy, 2010c). Taxa are then sampled and their frequencies summed to calculate a coverage value. Sampling stops when a desired level of coverage (= quorum) is reached. The quorum level is adjusted for each time bin via Good’s *u* (a value between 0 and 1), which is an estimate of sampling quality that corresponds to the proportion of occurrences of non-singleton taxa (Alroy, 2010b, 2010c). Therefore, each time bin can be subsampled to a maximum coverage, until the Good’s *u* value is reached. As such, it is more robust than other subsampling methods, such as classical rarefaction, that tend to flatten the estimated diversity curves (Alroy, 2010c; Close et al., 2018).

Coverage-based rarefaction, along with all data manipulation, was performed in R ver. 4.1.0 (R Core Team, 2021), using the tidyverse R package ver. 1.3.1 (Wickham et al., 2019). Eutherian and metatherian diversity were independently calculated with estimateD() from the iNext R package ver. 2.0.2 (Hsieh et al., 2020). This approach implements SQS based on the equations of Chao and Jost (2012), and extrapolation is based on the Chao1 estimator. Data were rarefied by collections and extrapolated estimates were limited to twice the sample size (as recommended in Hsieh et al. (2016). For the temporal analyses, diversity estimates were generated under three quorum levels (0.4, 0.6, and 0.8) as relative and rank-order diversity can vary depending on elected quorum level. In addition to generating diversity estimates for all terrestrial eutherian mammals, I also calculated SQS diversity of the main eutherian groups that comprise most of my dataset: caviomorph rodents, xenarthrans, and SANUs. Latitudinal analyses were incompatible with diversity estimates at higher quorum levels due to low sample size. I therefore focused my analyses on latitudinal diversity estimates under a quorum level of 0.4.

As variability in spatial sampling has the potential to bias reconstructions of global and latitudinal biodiversity trends (Close et al., 2020b; Flannery-Sutherland et al., 2022; Jones et al., 2021), I implemented a grid-cell rarefaction (GCR) approach (e.g. Close, Benson, Alroy, et al. (2020); Jones (2020) to test the impact on my continental diversity estimates. For each of the dataset replicates, and for each time bin, I randomly sampled (without replacement) five occupied equal-area grid cells (with 100 km spacings; Barnes and Sahr (2017)). Subsequently, I performed SQS (as described above) on collections intersecting with sampled cells. For each of the 100 dataset replicates, this process was repeated 100 times, and the mean of means was computed. This analysis found no considerable difference between continental biodiversity trends when analyses were conducted with and without GCR, and therefore I focus my results on those without GCR implemented (SI section 4).

PyRate

PyRate is an approach to estimating speciation, extinction, and preservation rates from fossil occurrence data, and has been implemented in a growing number of palaeobiological studies (e.g. Bacon et al. (2015); Carrillo et al. (2020); Huang et al. (2017); Pimiento et al. (2017); Silvestro, Castiglione, et al. (2019)). It applies Bayesian algorithms on occurrence datasets and calculates three sets of parameters, for every 1 Myr. Firstly, preservation rates (i.e. fossilization and sampling rates) are calculated based on the expected fossil occurrence count per sampled lineage per time unit. Secondly, based on these rates, speciation and extinction times are calculated for each taxon, which is important given that the true temporal extent of a species will almost certainly exceed its sampled (i.e. observed) range (Lee & Stenseth, 2007; Signor & Lipps, 1982). Finally, diversification rates are calculated, expressed as speciation and extinction rates (i.e. the expected number of speciation and extinction events per lineage per time unit), along with their temporal shifts. This is implemented with a birth-death model and can have temporal variability (i.e. rates can change for all groups at estimated times of rate shift) and taxon variability (i.e. rates can vary among taxa). PyRate then calculates the support of the different birth-death models on the data by calculating each model’s maximum likelihoods and comparing them using Bayes factors (Kass & Raftery, 1995).

Information on whether a taxon is extant is also required for PyRate – this information was extracted from the PBDB and validated based on the available literature. I chose a time-variable Poisson Process model of preservation, as this was the best-fitting model for my data according to the built-in command -PPmodeltest (SI section 4-5). I coupled this with a Gamma model to describe rate heterogeneity through time across taxa (using the -pP command). I also calculated individual lineage rates (using the -mG command), in addition to the rates of the whole dataset. I ran the PyRate analysis for 10,000,000 Reversible-Jump Markov Chain Monte Carlo generations (Green, 1995), sampling every 1000 generations, and I applied this to each of the 100 dataset replicates. I combined the resultant log files using the -combLogRJ and -combLog commands to obtain diversification and preservation rates, after removing the first 1000 generations as a burn-in period. PyRate analyses were performed on University College London's Myriad cluster, using PyRate ver. 0.5.0 in Python ver. 3.0 (Python Software Foundation, 2021).

Correlation tests

I tested for correlations between variables using ordinary least-square (OLS) regressions fitted by maximizing the log-likelihood and using the lm() function from base R. More specifically, I evaluated the contribution of individual eutherian groups (caviomorphs, xenarthrans, SANUs) on total eutherian diversity patterns through time. Similarly, I tested the correlation between subsampled eutherian and metatherian diversity through time, as well as the effect of global and regional palaeoenvironmental variables and Andean topography on sample-standardised eutherian diversity and diversification rates through time and space.

Results and Discussion

Observed diversity patterns

Cenozoic South American terrestrial eutherian mammal fossil occurrences are consistently rare at lower latitudes (although they are less rare in the Pleistocene), and the fossil record in the tropics is generally scarce (Figure 8A). Counts of observed genera and species have a strong, positive, statistically significant correlation with one another and with sampling proxies (i.e. number of occupied cells, collections, formations, and references; $R>0.9$, $p<0.001$). There are observed diversity and sampling peaks in the Bartonian (middle Eocene), Burdigalian (early Miocene), Tortonian (late Miocene), Zanclean (early Pliocene), and, most prominently, the Pleistocene (Figure 8C). There is also a strong, positive, statistically significant correlation between numbers of observed genera and Andean topography ($R = 0.84$; $p<0.001$). This potentially suggests that mountain building increases preservation potential, and that peaks in observed diversity might be artefacts of factors such as increased erosion during heightened orogenic activity. Sampling therefore appears to drive observed temporal and spatial diversity patterns, underlying the importance in accounting for it.

The three alpha diversity metrics produce broadly congruent results (SI section 2), and I herein discuss patterns based on the conservative cryptic approach (Figure 8B). Alpha diversity increases through time, but outliers (i.e. collections with exceptional diversity) are not exclusive to Recent times. For example, the middle Eocene Colhué-Huapi, the late Oligocene Cabeza Blanca, and the early Miocene Gran Barranca localities (all found at high latitudes) have a similar diversity as the early Pliocene Farola Monte Hermoso and Pleistocene Tarija localities (Figure 8B). Latitudinally, the highest alpha diversity levels are recorded in collections at high paleolatitudes (approximately 45–50°S), with an equatorward decline in alpha diversity, the exception to this is the Pleistocene where alpha diversity is more evenly distributed with latitude (Figure 8B). These results highlight the issue of uneven spatial fossil sampling across the continent, with

Patagonian localities more numerous and richer in fossils, and with a longer history of collection and studies.

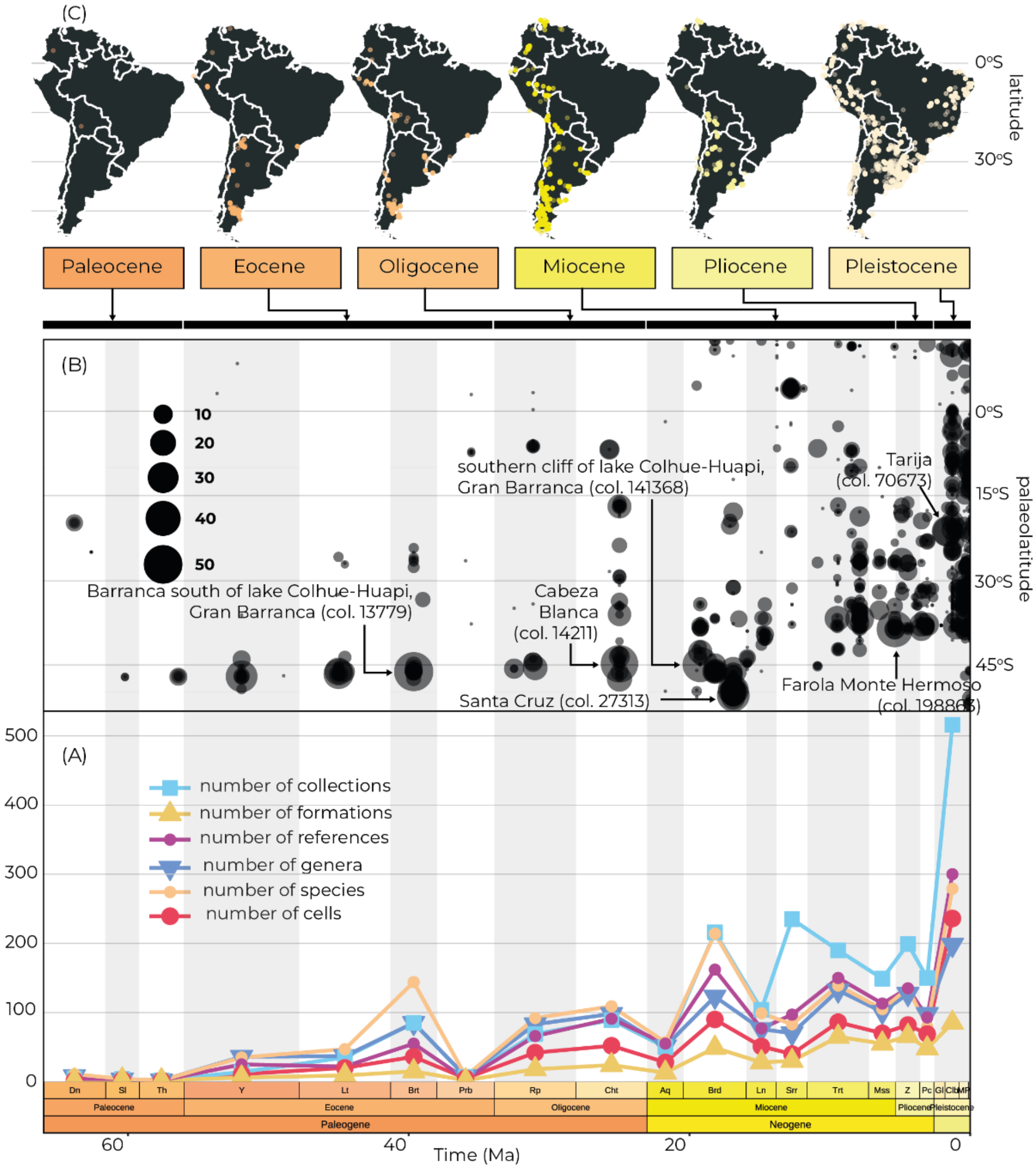

Figure 8: Spatio-temporal variation of fossil sampling and alpha diversity of eutherian mammals in South America. **(A)** Raw counts of different proxies of fossil sampling through time **(B)** cryptic alpha diversity (size of circles indicates cryptic diversity values) through time and latitude, and **(C)** Spatial distribution of fossil occurrences through time.

Sampling-corrected diversity patterns

A subtly different evolutionary history emerges after considering uneven sampling through time and space. Sample-standardised eutherian diversity shows a continuous rise throughout the Paleogene. The exception appears to be the Priabonian (late Eocene), but the exceptionally low extrapolated diversity for this time interval almost certainly reflects this stage's poor fossil record (Figure 9; SI section 5). Diversification rates initially increased and overall remained positive, with peaks in speciation rate occurring in the late Paleocene, Bartonian (middle Eocene), and early Oligocene (Figure 9). These results appear to reflect the initial arrival and subsequent radiation of eutherian mammals in South America in the aftermath of the Cretaceous/Paleogene mass extinction, 66 Ma, which has been termed the First American Biotic Interchange (Goin, et al., 2012a). Much of this initial radiation pertains to SANUs (Croft et al., 2020), with xenarthrans and caviomorph rodents increasingly contributing to South American diversity from the middle–late Eocene (Goin, et al., 2012a). The later Paleogene speciation peak likely reflects the 'Patagonian Hinge', a faunal turnover documented in the southern part of South America that has been linked with climate cooling (Goin et al., 2010). The end of the Paleogene is characterised by a diversification decline, resulting from an increase in extinction rate.

During the earliest Neogene, there is a subsequent peak in diversification, resulting from a rise in speciation rate in the Aquitanian and Burdigalian (early Miocene). Speciation and extinction are largely constant throughout the remainder of the Miocene, but there is a diversity decline in the first middle Miocene, reaching the lowest value of the Neogene (Figure 9)**.** The Tortonian (early late Miocene) and early Pliocene are characterized by high eutherian diversity, with a decline in the latest Miocene (Messinian); see also Carrillo et al. (2020). Extinction rates spike in the late Pliocene and the late Pleistocene, producing a diversity decline towards the Recent (Figure 9).

SANUs, xenarthrans, and caviomorphs all peak in diversity in the Oligocene, with SANUs reaching their zenith (Figure 9). This is followed by a decline in all groups, until the late middle Miocene and a recovery in the late Miocene. The decline in SANU diversity results from the disappearance of Pyrotheria in the late Oligocene, and Astrapotheria in the middle Miocene (Croft et al., 2020). The late Miocene recovery in SANU diversity is driven by Notoungulata and Litopterna, prior to the total extinction of SANUs, with the last representatives (including the litoptern *Macrauchenia* and notoungulate *Toxodon*) part of the late Pleistocene megafaunal extinctions (Croft et al., 2020; Goin, et al., 2012a). Xenarthrans show their highest diversity in the late Pliocene but decline afterwards (Figure 9), representing one of the most affected groups in the megafaunal extinctions in South America (Barnosky & Lindsey, 2010). Caviomorphs are the only major South American eutherian group whose diversity recovers in the Pleistocene, which is reflected by the relatively high proportion the group represents in present-day South American ecosystems (Vucetich et al., 2015).

Some of the overall eutherian diversity patterns are similar to those of other vertebrate groups in South America. Turtle diversity patterns are broadly similar to those of eutherians, with the exception that the former group's diversity increased in the Pleistocene (Vlachos et al., 2018). Crocodylian diversity peaked in the middle–late Miocene on the continent, before declining thereafter (Mannion et al., 2015; Scheyer et al., 2013). However, whereas fluctuations in crocodylian diversity seem to correspond with the evolution of the western Amazonia Pebas mega-wetland system (Salas-Gismondi et al., 2015), no such clear link has been found for eutherians (Antoine et al., 2017). By contrast, metatherians show an overall decline in diversity during the Cenozoic (SI section 11; Bennett et al. (2018); Tarquini et al. (2022)), leading to their relatively low representation in present-day South American ecosystems. In general, metatherians have low diversity wherever they are found with eutherians, probably due to the former group's developmental characteristics that renders them less energy-efficient and less adaptable (Bennett & Goswami, 2013; Goin et al., 2016; Goswami et al., 2016).

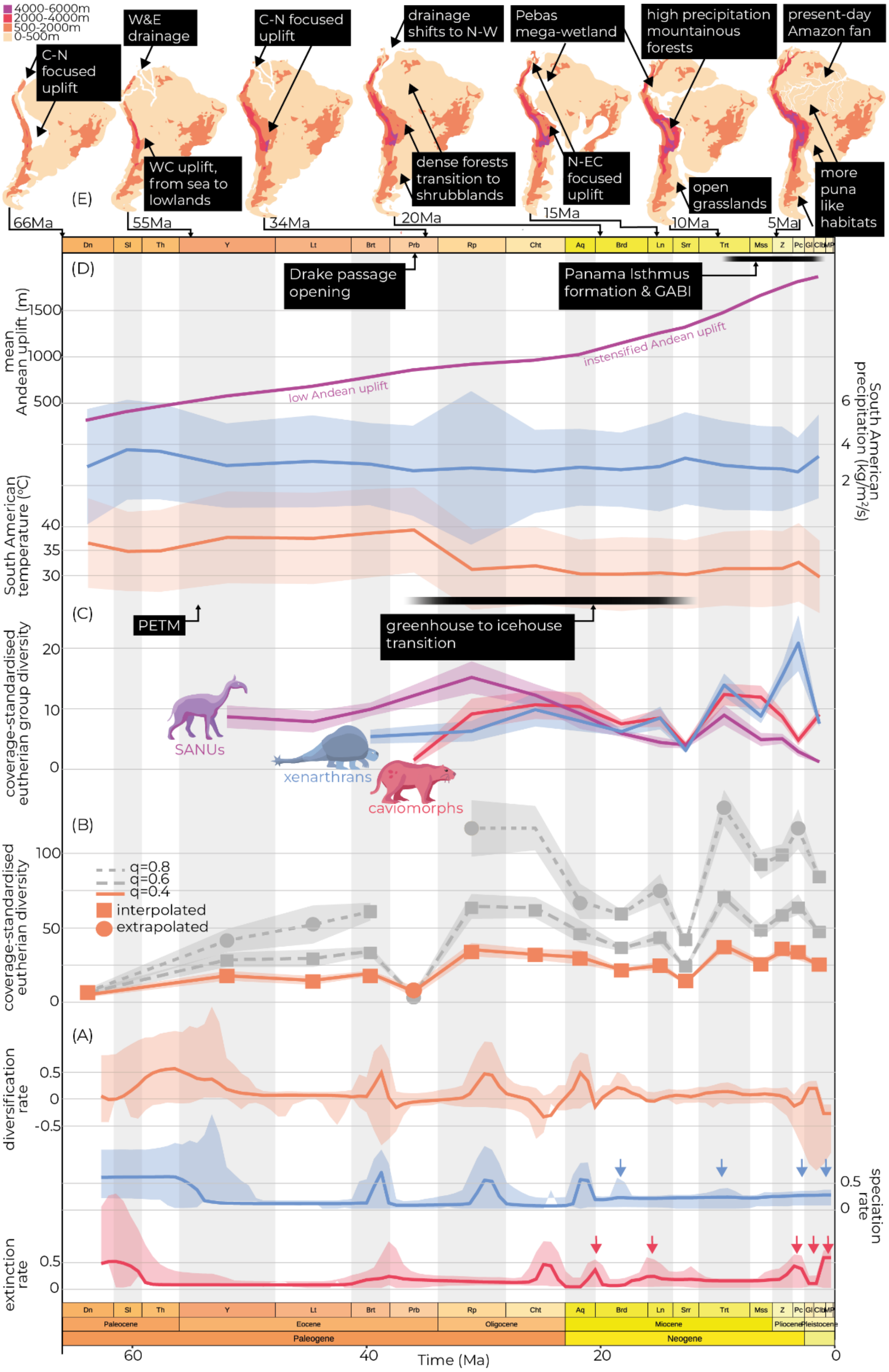

Figure 9: Eutherian mammal diversity and environmental changes in South America through time. **(A)** extinction, speciation and diversification rates, calculated by PyRate - the arrows indicate instances of rate shifts supported by a strongly significant posterior probability of rate shift (logBF > 6). Shaded area represents confidence intervals. **(B)** Coverage-based diversity for all eutherian mammals (for quora 0.4, 0.6, and 0.8), and for **(C)** the main eutherian groups Notoungulata (here indicated by a litoptern illustration),

Xenarthra (here illustrated by a glyptodont illustration), and caviomorph rodents (here indicated by a *Phoberomys* illustration), for quorum level 0.4. **(D)** South American mean annual temperature and precipitation (both calculated using the HadCM3 models) and mean Andean uplift, based on Boschman (2021) and Boschman & Condamine (2021). Shaded area represents maximum and minimum values. **(E)** Elevation maps of South America for 66, 55, 34, 20, 15, 10, and 5Ma. Andean topology from Boschman (2021). Marine incursions based on Wesselingh & Hoorn (2011) and Hernandez et al. (2005) for Amazonia and south-eastern South America respectively. River system illustrated in 55 and 34Ma maps are strictly speculative, used to illustrate direction of drainage. The Amazonian river system in 5Ma map is based on the present-day. C: central, N: northern, E: eastern, W: western parts of the Andes.

Tectonic, environmental, and biotic drivers

I found no statistically significant correlation between sample-standardised diversity through time and any of the tested palaeoenvironmental variables, including continental-scale topography (SI section 9). However, Andean topography is significantly correlated with eutherian sample-standardised diversity through time (slope = 0.012, p = 0.0169, Adjusted R^2 = 0.2975; Figure 9). Coupled with the positive correlation with observed diversity (see above), this suggests that mountain building acts as a ‘common cause’ on land (*sensu* Peters, 2005), shaping both my sampling of diversity, as well as diversity itself. When this correlation is evaluated individually for each of the three main groups of South American eutherians (Adjusted R^2 = 0.7577), I recover positive, but statistically non-significant correlations for xenarthrans (slope = 26.11, p = 0.056) and caviomorphs (slope = 32.06, p = 0.213), but a significant negative correlation between Andean topography and sampling-standardised diversity of SANUs through time (slope = -65.8, p = 0.004).

The lack of recovery of a statistically significant correlation between continental-scale South American topography and temporal diversity could be because it was topographical changes in the Andean region only, and not the whole of the continent, that drove diversity shifts (SI section 9). On the other hand, the lack of correlation between the tested palaeoenvironmental variables and temporal diversity patterns does not necessarily reject climate as a driver of South American eutherian diversity.

The formation of the Andes played a key role in transforming the South American continental climate, working in tandem with global climate cooling (Palazzesi et al., 2014). More specifically, the Andes formed a barrier that extended from the continent's highest to lowest altitudes; this prevented Pacific humid winds from reaching the central and eastern parts of the mountain chain, thus promoting aridification in those regions, while increasing precipitation in the western side of the mountain range (Cione et al., 2015a; Figueiredo et al., 2009; Hoorn, Wesselingh, ter Steege, et al., 2010; Insel et al., 2010; Ortiz-Jaureguizar & Cladera, 2006; Pascual & Odreman-Rivas, 1973; Poulsen et al., 2010; Quattrocchio et al., 2003; Rech et al., 2006). It is likely that the palaeo-temperature and -precipitation variables do not adequately capture these regional, albeit key, climatic shifts for South America, because of their coarser scale.

Mountains generally provide a broad range of habitats, and are linked with high diversity (Badgley et al., 2017; Hoorn et al., 2018; Perrigo et al., 2020). Today, the Andes Mountains are one of the globe's biodiversity hotspots, hosting the highest number of vertebrate and plant species (Myers et al., 2000), and its evolution is thought to have played an important role in this richness (Antonelli et al., 2018; Boschman & Condamine, 2022; Hoorn, Wesselingh, ter Steege, et al., 2010; Pérez-Escobar et al., 2022). Andean uplift has been diachronous (Boschman, 2021; Figure 9E), and sections of the mountain range have been subject to different tectonic forces (Gianni et al., 2018; Pérez-Escobar et al., 2022; Schepers et al., 2017). The overall early rise in South American eutherian diversity coincides with relatively low Andean uplift rates, which primarily occurred in the central and northern parts of the mountain range (Boschman, 2021; Boschman & Condamine, 2022). During this interval, west-central regions of the mountain chain that had been marine basins (Boschman, 2021) became low-altitude terrestrial regions (Hoorn, Wesselingh, ter Steege, et al., 2010).

Eutherian mammals experienced increased extinction rates, that could potentially be linked with the habitat changes that took place at the end of the Paleogene, as South America experienced a >5 ^{o}C drop in temperature, dense forests started to be replaced by open shrublands in the southern parts of the continent (Dunn et al., 2015), and drainage systems changed in northern and central South America, with east-west flowing rivers shifting to a northwest flow direction (Figueiredo et al., 2009; Hoorn, Wesselingh, ter Steege, et al., 2010; Sena Costa et al., 2000). Mountain building intensified in the Miocene onwards, occurring mainly in the northern and, most notably, east-central Andes (Boschman, 2021; Boschman & Condamine, 2022; Tournier et al., 2020), coinciding with overall positive diversification rates in the Miocene, the exception being the Langhian (middle Miocene), a period characterised by extensive marine transgressions in South America (Hernández et al., 2005; Wesselingh & Hoorn, 2011), and during which eutherians experienced an extinction rate peak.

The late Miocene eutherian diversity peak coincides with an estimated elevation increase of ~2500m between 9.1 and 3.8 Ma, with mountainous forests characterised by high precipitation in the central parts of the Andes (Martínez et al., 2020). It is also synchronous with the initial development of the Amazonian river system in northern-central South America (Bicudo et al., 2020; Figueiredo et al., 2009; Mora et al., 2010; Sacek, 2014), as well as the emergence of primarily open grassland habitats in the Patagonian region (Dunn et al., 2015; Palazzesi & Barreda, 2012; Strömberg et al., 2013). Carrillo et al. (2020) recovered a similar late Miocene diversity peak, which they attributed primarily to fossil occurrences emanating from the Ituzaingó formation (Brunetto et al., 2013; Cione et al., 2000). Although those authors considered the possibility that this might be a sampling artefact, these results support their preferred interpretation that the late Miocene represents a genuine diversity increase in South American eutherian mammals (e.g. caviomorphs; see below).

The eutherian diversity decline in the Pliocene onwards took place during a more intensified phase of Andean uplift, including a north-eastward (Ecuador) and central-westward uplift migration, reaching the Sub-Andean and Sierras Pampeanas regions (Boschman, 2021; Boschman & Condamine, 2022), habitat shifts (including the appearance of more puna-like ecosystems; Martínez et al., 2020), and an important climate shift: South American mean annual temperature reached its lowest value around that time, dropping from 26 °C in the late Pliocene to 23 °C in the Pleistocene (Figure 9). Similarly, mean annual precipitation reached its highest late

Cenozoic value (probably related to the appearance of high precipitation mountainous areas in central Andes; Martínez et al., 2020), increasing from 2.7 kg/m^2/s in the late Pliocene to 3.4 kg/m^2/s in the Pleistocene (Figure 9).

Although my analyses do not directly test the effect of the GABI, with its main phases taking place in the Pliocene and Pleistocene (Carrillo et al., 2020), broad patterns can be observed. The diversity decline of South American mammals occurred primarily in southern South America (Carrillo et al., 2020), and has been attributed to stresses induced by the GABI arrivals (e.g. competition, higher susceptibility to predation, transmission of pathogens), as well as from ongoing climatic changes (Carrillo et al., 2020; Faurby & Svenning, 2016; Morgan, 2008; Webb, 1985; Woodburne, 2010). Caviomorph diversity was in decline during the Pliocene (Figure 9), including the loss of lineages belonging to Dinomyidae, Echimyidae, Erethizontidae, as well as the extinction of Neoepiblemidae (Vucetich et al., 2015). On the other hand, xenarthran diversity peaked in the Pliocene. The group's resilience to North American newcomers (as well as their own dispersal success into North America) has been attributed to their unique characteristics, including their flexible and expanded diet, resulting from their dental complexity (Castro et al., 2015; Ciancio et al., 2014; Vizcaíno, 2009), as well as their relatively low metabolic rates (McNab, 1985). Xenarthrans also evolved a high diversity of gigantic forms in the Pliocene, including sloths, glyptodonts and pampatheres, that could have rendered them more resilient towards predation and competition with the new GABI arrivals (Faurby & Svenning, 2016), although they went extinct in the Pleistocene megafaunal extinctions (Patterson et al., 2013), possibly as a result of human predation (e.g. Carlini et al. (2022)).

The reasons leading to the extinction of the last SANUs in the Pleistocene are still unclear. Previous studies have pointed to the rise of competition due to the arrival of Proboscidea, Perissodactyla and Artiodactyla from North America during the GABI (Webb, 1976), and/or their increased susceptibility to predation by newly arrived carnivorans (Carrillo et al., 2020; Faurby & Svenning, 2016; Patterson & Pascual, 1968). However, these hypotheses cannot explain the long-term decline of SANUs from the late Oligocene onwards (Figure 9). The results of this thesis suggest that Andean uplift, and its concomitant dramatic habitat reshaping, was the key factor in their long-term decline. The highly unusual morphologies of SANUs, like the earlier appearance of hypsodonty (potentially linked with the evolution of the Andes (Dunn et al., 2015; Kohn et al., 2015; Strömberg et al., 2013)), in conjunction with their overall lower diversity (compared to xenarthrans and caviomorphs), might have led to a greater susceptibility of some clades to rapid habitat changes. For example, sedimentological and bone microstructural evidence support a semi-aquatic habitat for astrapotheres (Carrillo et al., 2018; Houssaye et al., 2016), and it is likely that changes in the drainage pattern of the Pebas mega-wetland system contributed to their extinction in the middle Miocene (Antoine et al., 2017; Hoorn, Wesselingh, ter Steege, et al., 2010). Interestingly, Andean uplift has also been proposed as one of the key factors driving the decline of sparassodont metatherians in the second half of the Cenozoic (Pino et al., 2022; Tarquini et al., 2022). It has also been suggested to have acted as the driver of the deep-time high diversification of some amphibian and reptile groups in the Paleogene and Neogene (Boschman & Condamine, 2022).

The emergence of the present-day latitudinal biodiversity gradient

Sample-standardised eutherian diversity is reconstructed as highest at mid-latitudes (30° to 45° S) during the Paleogene and early–middle Miocene (Figure 10). In the late Miocene, diversity is highest in the 15° to 30° S latitudinal band. Although the Pliocene record is not rich enough at low latitudes to reconstruct a diversity gradient, sample-standardised eutherian diversity is highest at 0° to 15° S in the Pleistocene. Fossil sampling is generally patchy in lower latitudes of South America (Carrillo et al., 2015), and thus is difficult to compare diversity between tropical and temperate latitudes with confidence. However, focusing on the better sampled latitudinal bands, diversity declines within high latitudes from the early–middle Miocene, to the Recent (Figure 10). Sampling improves towards the Recent (Carrillo et al., 2015), suggesting that these results have less probability of being artefacts of the uneven preservation of fossils latitudinally. My results suggest that the South American terrestrial LBG was potentially flatter than the present-day during the early Cenozoic. They suggest that the LBG began to steepen in the late Miocene, with the present-day gradient forming at some point during the Plio-Pleistocene, i.e. in the last 5 Myr. This is broadly congruent with the emergence of the present-day LBG in continental North America, estimated to have formed approximately 4 Ma (Marcot et al., 2016).

Potential LBG drivers dan be summarized as geographical, historical, and climatic (see also Mittelbach et al. (2007); Pontarp et al. (2019); Willig et al. (2003)), with the fossil record providing an unparallel perspective with which to tease apart competing hypotheses (Brodie & Mannion, 2022). Geographical drivers refer to greater areal extent enabling higher diversity in the tropics (Rosenzweig, 1995). Although South America holds greater area extent towards the tropics, this has been the case throughout the last 66 Myr, and so this cannot explain the emergence of the present-day LBG only in the last 5 Myr. Furthermore, no statistically significant correlation was found between diversity and land area with latitude in any time interval in my thesis.

Historical drivers are those that involve higher tropical diversity building up over longer uninterrupted time intervals, as a consequence of relatively limited environmental perturbations (Willig et al., 2003). Although Andean uplift, a key driver of the continent’s reshaping, had a less prominent effect in the southern parts of the continent (see above), other tectonic-driven shifts were taking place that did affect this region, namely the separation of South America and Antarctica in the Paleogene (Livermore et al., 2005), resulting in the formation of the Drake Passage during the Eocene/Oligocene transition (Barker & Burrell, 1977; Scher & Martin, 2006b; Toumoulin et al., 2020). This led to the development of the Circumpolar Current (Livermore et al., 2004), which amplified ongoing cooling and aridification in southern South America, as well as ice sheet expansion in Antarctica (Goin, et al., 2012a; Miller et al., 1987; Mudelsee et al., 2014; Passchier et al., 2013; Prothero et al., 2003). This shift to colder, drier, and more seasonal habitats coincided with the ‘Patagonian Hinge’ (Goin et al., 2010). Thus, these environmental perturbations and faunal disruptions at higher latitudes might have played a role in shaping the present-day South American LBG, but lower latitudes were not environmentally or tectonically stable either.

Climate has often been considered as the main driver of the LBG, with a higher concentration of taxa in the tropics, with specialised, restricted niches as a consequence of lower seasonality and higher insolation and productivity (Archibald et al., 2010; Mittelbach et al., 2007; Willig et al., 2003). Furthermore, the presence of a unimodal LBG (i.e. the present-day pattern) has been linked with periods of icehouse worlds, i.e. intervals characterised by a steeper latitudinal temperature gradient and higher seasonality (Kröger, 2017; Mannion et al., 2014). With the transition to an icehouse world in the late Paleogene (a period of warm climate, and extensive temperate diversity like the presence of monkeys in Patagonia; Silvestro, Tejedor, et al. (2019)), and a continued global cooling trajectory into the Neogene (Westerhold et al., 2020; Zachos et al., 2008), and the further cooling and precipitation increase in the Plio-Pleistocene transition, the absence of a unimodal LBG in South America until the last 5 Myr, fits this scenario. Moreover, I found that the latitudinal distribution of mean annual temperature (slope = 0.765, p = 0.015) and mean annual precipitation (slope = -4.329, p = 0.027) correlate with eutherian diversity in the Pleistocene. The importance of precipitation, alongside temperature, has previously been recognised in constraining the distribution of diversity (Saupe, Myers, et al., 2019), including for North American Cenozoic mammals (Fraser et al., 2014). In the late Pleistocene, in particular, Saupe, Myers, et al. (2019) showed that the effect of precipitation shifts on diversity were more intense at lower latitudes, whereas temperature shifts were more intense at higher latitudes. Although the absence of such a correlation in earlier time periods could be a result of less complete fossil sampling, my data show that there was a major tropical precipitation increase in the Pliocene/Pleistocene transition of South America from 2.9 to 4.9 kg/m^2/s in the 0° to 15° N latitudinal band (perhaps related to the Andean uplift of these regions), and a 2.5 to 3.3 kg/m^2/s increase in the 0° to 15° S band (SI section 13). Temperature and precipitation are therefore potentially key drivers of the South American LBG pattern, at least in the Plio-Pleistocene. Climate was also underlined as the main driver in North America, with a strengthened gradient linked with global cooling (Marcot et al., 2016).

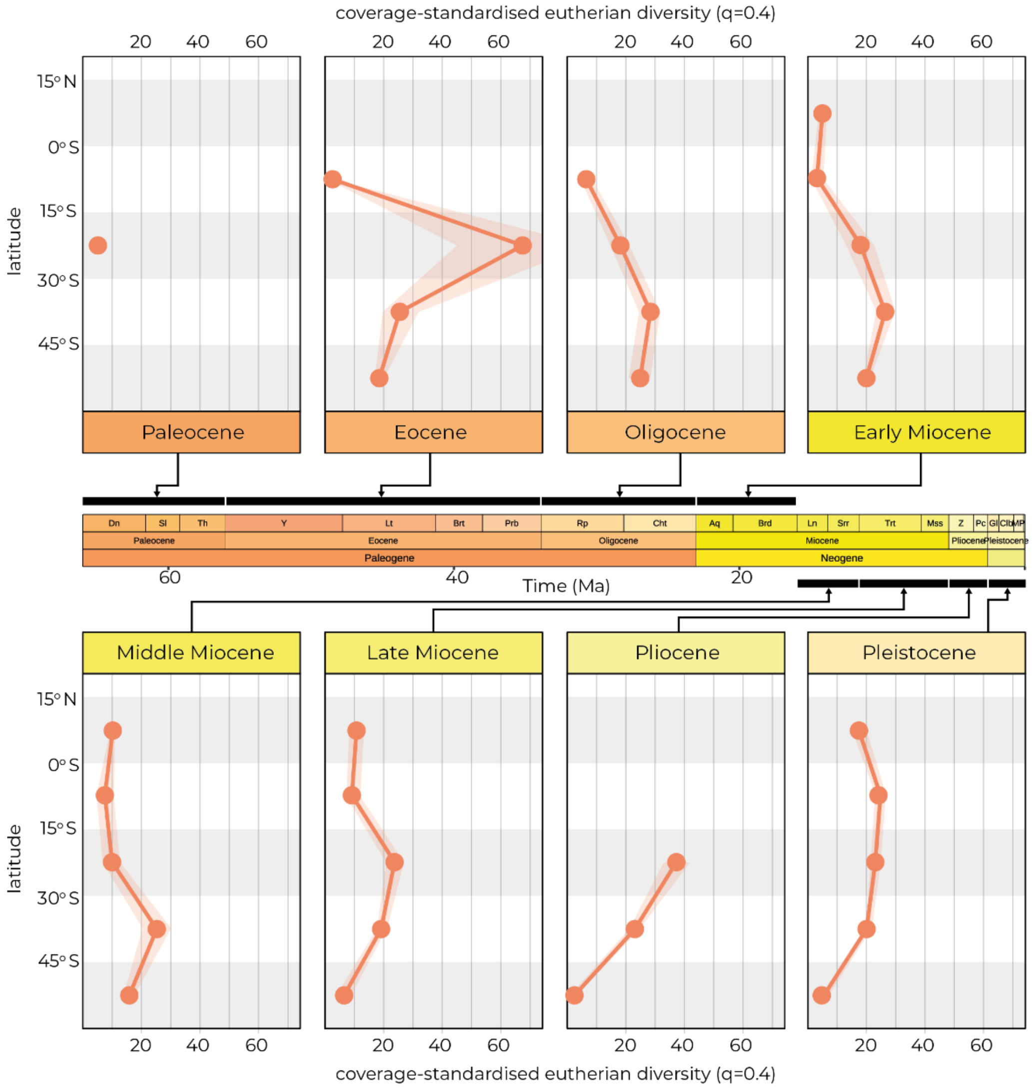

Figure 10: Spatial eutherian subsampled diversity (for quorum level = 0.4), using 15 degree latitudinal bins, for the Paleocene, Eocene, Oligocene, Early Miocene, Middle Miocene, Late Miocene, Pliocene, and Pleistocene.

The Plio-Pleistocene appearance of the present-day LBG also coincides with the main phases of the GABI. Although Marcot et al. (2016) discarded the GABI as a key driver of the LBG in North America, due to the relatively low number of South American groups reaching North America, this is not the case for South America. The GABI was asymmetrical, with disproportionately more North American taxa reaching South America

(Bacon et al., 2015; Webb & Marshall, 1982), or at least a greater number of species successfully establishing themselves on the southern landmass (Carrillo et al., 2020). However, the Plio-Pleistocene fossil record of tropical South America shows that North American mammals did not dominate these ecosystems, and their representation was in fact much greater at higher latitudes in South America (Carrillo et al., 2018; Carrillo-Briceño et al., 2021), with a possible dispersal corridor forming via Andean uplift, facilitating the movement of North American groups reaching the central and southern-most parts of South America (Patterson et al., 2012). As such, higher South American diversity at low latitudes did not result from increased North American emigrants into the tropics, although heightened extinction of South American eutherians, in the southern parts of the continent, due to competition with North American emigrants, likely contributed to the steepening of the LBG. Regardless, my results indicate a primary role for climate in shaping the emergence of the South American terrestrial LBG.

Conclusion

The findings of this thesis have shed light on the multi-faceted and deep-time relation between terrestrial vertebrate diversity and climate and topography, in South America, one of the continents most affected by the current climate crisis. Andean uplift, along with its subsequent habitat and climate remodelling taking place throughout the Cenozoic, drove eutherian mammal diversity in South America, aiding some groups to diversify, while others to perish. In addition, precipitation and temperature likely played a key role in the emergence of the present-day terrestrial mammalian LBG in the last 5 Myr, similar to that of North America. While there are still plenty of aspects of the diversity-climate relationship to explore, like the role of the GABI in the shaping of the LBG, this thesis’s findings contribute towards a better understanding, and empirical evidence of the biodiversity-climate relationship, that is critical in the light of the current climate crisis.

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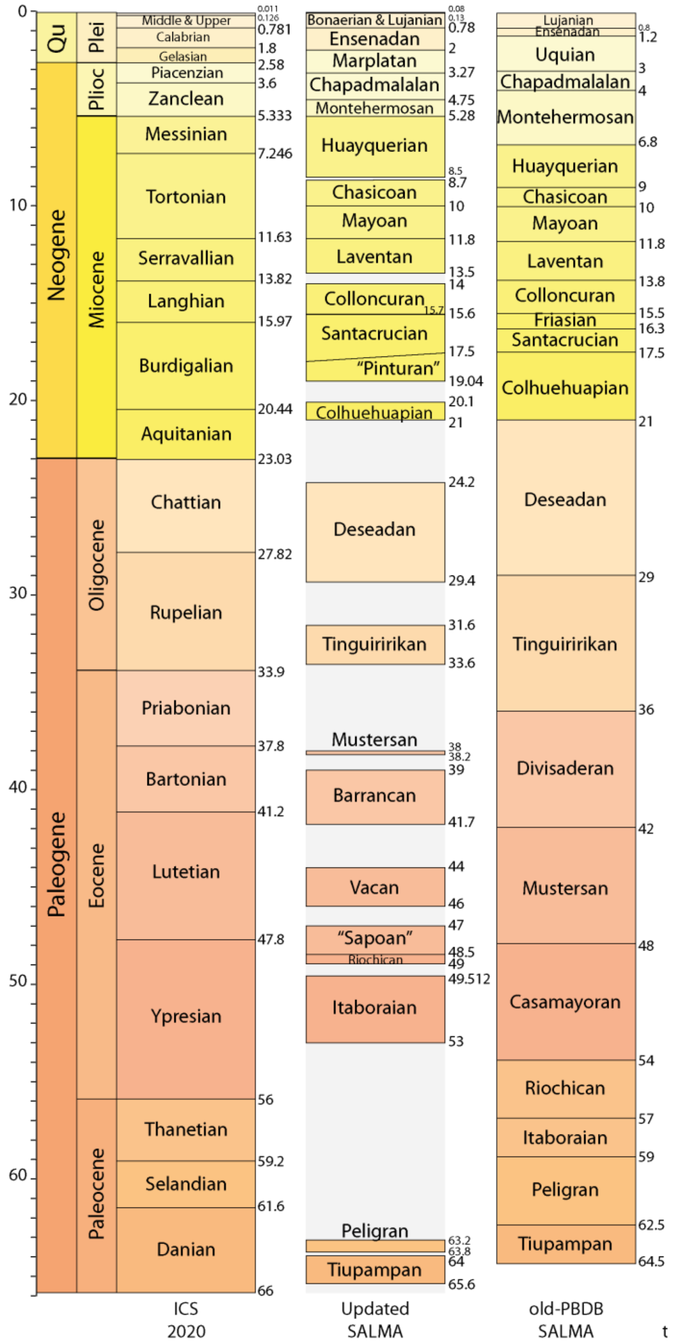
Supplementary Information

1. Updating the SALMAs

The International stages (International Commission of Stratigraphy or ICS, 2020) are compared to the out-of-date SALMAs from the PBDB and the updated SALMA from this study.



For the latter, I have performed a literature review to extract the most recent information on the SALMAs age limits. The first column has the SALMA names currently used in the literature. The next two columns have the updated lower (max Ma) and upper (min Ma) boundaries for each SALMA. The fourth column shows the references used for each SALMA. Finally, the last column presents the SALMA names used in the PBDB – some are outdated and replaced (example the Uquian) and those are indicated in bold.

Current SALMAs	max (Ma)	min (Ma)	Notes & references	Old-PBDB SALMAs
Lujanian	0.13	0.08	(Cione & Tonni, 1999; Pardiñas et al., 2004; Tonni et al., 2003)	Lujanian
Bonaerian	0.78	0.13	(Cione & Tonni, 1999; Verzi et al., 2004)	Lujanian
Ensenadan	2	0.78	Upper Ensenadan ~ 0.78Ma (MacFadden et al., 1983) for upper limit of Ensenadan age: Ensenadan/ Marplanan ~2Ma (Cione & Tonni, 1995, 1999)	Ensenadan
Marplatan	3.27	2	Ensenadan/ Marplanan ~2Ma (Cione & Tonni, 1995, 1999) Marplatan/ Chapadmalalan 3.27Ma (Schultz et al., 1998; Tomassini et al., 2013; Zárate, 2005)	Uquian
Chapadmalalan	4.5-5	3.27	Marplatan/ Chapadmalalan 3.27Ma Chapadmalalan/ Montehermosan 4.5/5Ma (Tomassini et al., 2013; Zárate, 2005)	Chapadmalalan
Montehermosan	5.2-8	4.5-5	Chapadmalalan/ Montehermosan 4.5/5Ma (Tomassini et al., 2013; Zárate, 2005) Montehermosan/ Huayquerian: base of Montehermosan at 7.1Ma (Reguero & Candela, 2011) but new findings do not support the 6.8/7Ma extension, but a 5.28Ma age (Tomassini et al., 2013)	Montehermosan
Huayquerian	8.5	5.28	(Tomassini et al., 2013) 8.5 Ma (Cione & Tonni, 2001; Reguero & Candela, 2011)	Huayquerian
Chasicoan	10	8.7	Upper limit <9.02 (8.7) Ma (Zárate et al., 2007) and lower limit ~10Ma (>10Ma) (Cione et al., 2000; Cione & Tonni, 2005; Zárate et al., 2007)	Chasicoan
Mayoan	11.8	10	11.8–10Ma (Flynn & Swisher III, 1995)	Mayoan
Laventan	13.5	11.8	13.5–11.8Ma (Madden et al., 1997)	Laventan
Colloncuran	15.7	14	15.7–14Ma (Bondesio et al., 1980; Madden et al., 1997; Marshall et al., 1977)	Colloncuran
Santacrucian	18	15.6	18–15.6 Ma (Cuitiño et al., 2016; Fleagle et al., 2013; Perkins et al., 2012)	Friasian Santacrucian
Pinturan?	19.04	17.5	19.04 to 17.5 Ma (Dunn et al., 2013)	Colhuehuapian
Colhuehuapian	21	20.1	21.0– 20.1 Ma (Dunn et al., 2013)	Colhuehuapian
Deseadan	29.4	24.2	29.4–24.2 (Dunn et al., 2013)	Deseadan
Tinguirirican	33.6	31.6	33.6–31.3 Ma (Dunn et al., 2013)	Tinguirirican
Mustersan	38.2	38	38.2– 38 (Dunn et al., 2013)	Divisaderan
Barrancan (Casamayoran subage)	41.7	39	41.7 to 39.0 Ma (Dunn et al., 2013)	Casamayoran
Vacan (Casamayoran subage)	46	44	46-44 Ma (Woodburne, Goin, Bond, et al., 2014)	Casamayoran
“Sapoan”	48.5	47	48.5 – 47 Ma (Tejedor et al., 2009; Woodburne, Goin, Raigemborn, et al., 2014)	Mustersan?
Riochican	49	48.5	49 Ma – 48.5 Ma (Woodburne, Goin, Raigemborn, et al., 2014)	Riochican
Itaboraian	49.512	53	49.512 Ma – 53 Ma (Woodburne, Goin, Raigemborn, et al., 2014)	Itaboraian

Peligran	63.2	63.8	63.2 – 63.8 Ma (Clyde et al., 2014; Woodburne, Goin, Raigemborn, et al., 2014)	Peligran
Tiupampan	64	65.6	64Ma – 65.6 Ma (Woodburne, Goin, Bond, et al., 2014)	Tiupampan

2. Alpha diversity

I calculated alpha diversity or local richness by counting the number of unique species in each collection (or fossil locality).

I also incorporated “cryptic diversity” by looking at occurrences indeterminate at species level in each collection and counting potentially distinct species using the occurrence’s higher taxonomic classification in the PBDB. Thus, we used the identified name of occurrences classified in all levels (species to order) to calculate cryptic alpha diversity.

Cryptic diversity, while it can be very informative, has often been overlooked in the fossil record, with a few exceptions (Close et al., 2019; Dunne et al., 2018; Mannion et al., 2011).

Here, I calculate cryptic alpha diversity in two ways. The relaxed approach was performed similarly to that in other papers (Close et al., 2019; Dunne et al., 2018). These authors also refer to it as indeterminate richness. It is a less conservative approach, where diversity equals the number of unique occurrence names, with vaguely classified occurrences (i.e. not in species level, example Genus sp. or Family indet.) counting as separate species.

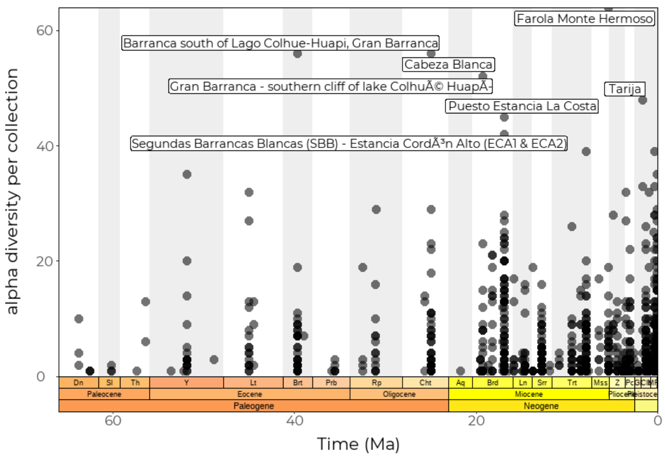
I also calculate cryptic alpha diversity in a more conservative approach (resembling that of Mannion et al., (2011)). Occurrences that are not classified at species level are considered distinct only if they belong to an order not already represented in the collection. Counts per collection are expected to be lower than the previous approach.

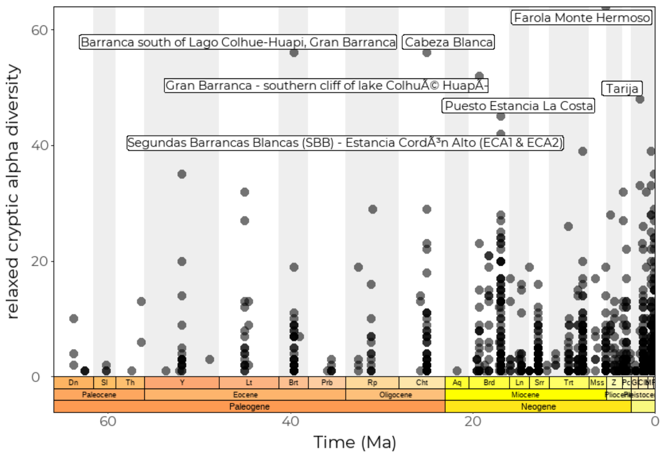
Note that both approaches consider occurrences with cf. aff. ? etc. as the same species (for example *Macrauchenia cf. patagonica* is considered the same species as *Macrauchenia patagonica*). In both approaches, informal species (e.g. <sp. A>, <sp. B> etc.) are also not considered distinct species.

In the following example on a fossil collection, alpha diversity (excluding cryptic diversity) would be equal to 1, as the only recognised species for this collection would be *Macrauchenia patagonica.* However, the conservative cryptic alpha diversity for the same collection would be equal to 2, recognising the additional distinct species Toxodontia indet. Finally, the relaxed cryptic alpha diversity would equal 4, in addition recognising *Macrauchenia sp.* and Macrauchenidae indet. as distinct species.

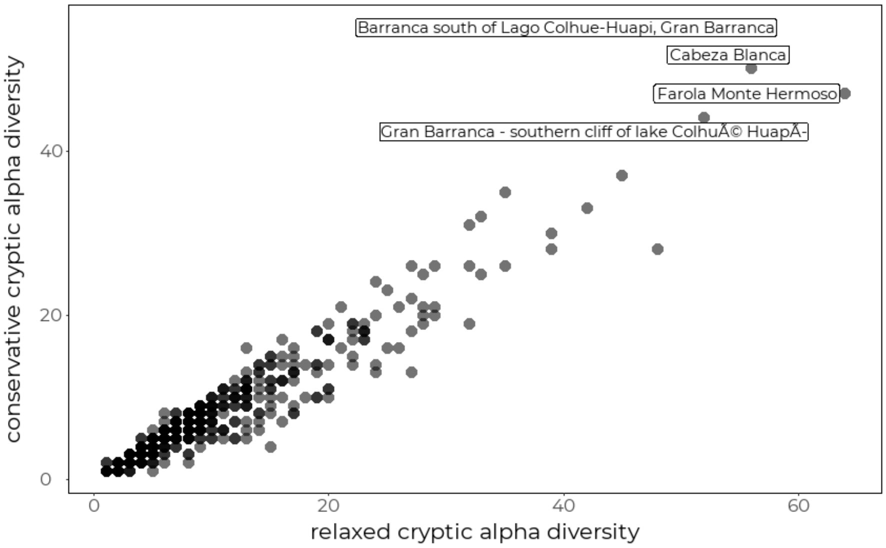
Order	Occurrence
Litopterna	*Macrauchenia patagonica*
Litopterna	*Macrauchenia* cf. *patagonica*
Litopterna	*Macrauchenia sp.*
Litopterna	*Macrauchenia* <sp. A>
Litopterna	*Macrauchenia* <sp. B>
Litopterna	Macrauchenidae indet.
Toxodontia	Toxodontia indet.

Alpha diversity, as well as “relaxed” cryptic alpha diversity is calculated and plotted in the following graphs.





In the following graph is shown the relation between the “relaxed” cryptic alpha diversity versus the “conservative” cryptic alpha diversity. The points are collections, and this graph shown an obvious correlation, especially in collections with less diversity.



3. Raw counts

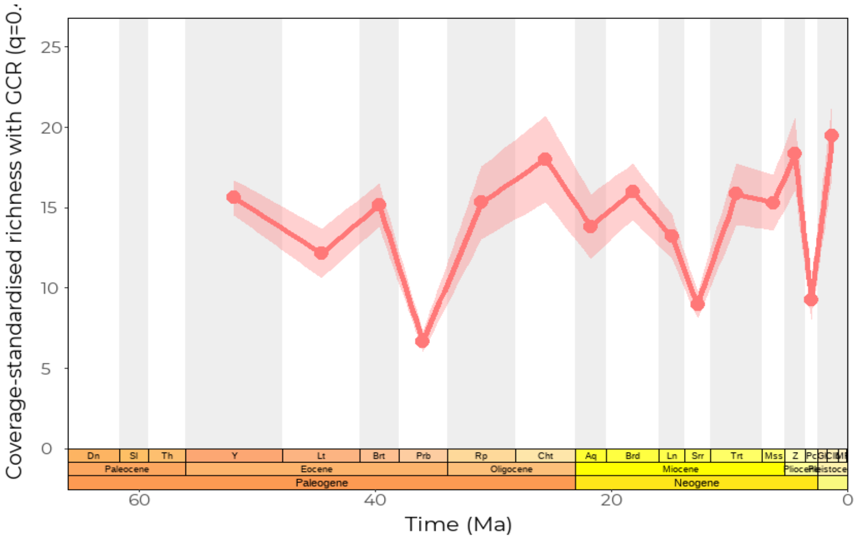
In the following table are shown raw counts of cells, collections, references, genera and species per time bin. Cell counts are correlated with genera counts (Rho = 0.967, p < 0.001). Same for collection counts vs genera (Rho = 0.881, p < 0.001) and for reference counts vs genera (Rho = 0.947, p < 0.001). Spearman’s test showed very positive (Rho = 0.931) and statistically significant (p < 0.001) correlation between accepted genera mean counts and accepted species mean counts. Therefore, it would be redundant to do all analyses for both genera and species level. I run them only in genus level because I believe that species counts are more prone to taxonomic bias.

name	max_age	min_age	mid_age	bin	genus_mean	collections_mean	species_mean	references_mean	cells_mean
Pleistocene	2.588	0.0117	1.29985	18	198	516	279	300	236
Piacenzian	3.6	2.588	3.094	17	98	150	80	93	66
Zanclean	5.332	3.6	4.466	16	127	199	135	135	85
Messinian	7.246	5.332	6.289	15	101	149	105	113	76

Tortonian	11.62	7.246	9.433	14	132	190	139	150	77
Serravallian	13.82	11.608	12.714	13	70	235	83	97	37
Langhian	15.97	13.82	14.895	12	76	104	99	77	47
Burdigalian	20.44	15.97	18.205	11	123	216	214	162	94
Aquitanian	23.03	20.44	21.735	10	51	50	57	55	26
Chattian	28.1	23.03	25.565	9	98	89	109	91	49
Rupelian	33.9	28.1	31	8	83	69	92	66	44
Priabonian	38	33.9	35.95	7	8	7	8	4	7
Bartonian	41.3	38	39.65	6	85	85	144	55	36
Lutetian	47.8	41.3	44.55	5	37	35	47	22	16
Ypresian	56	47.8	51.9	4	36	14	35	25	11
Thanetian	59.2	56	57.6	3	2	2	2	2	3
Selandian	61.6	59.2	60.4	2	3	4	4	4	3
Danian	66	61.6	63.8	1	8	5	11	4	2

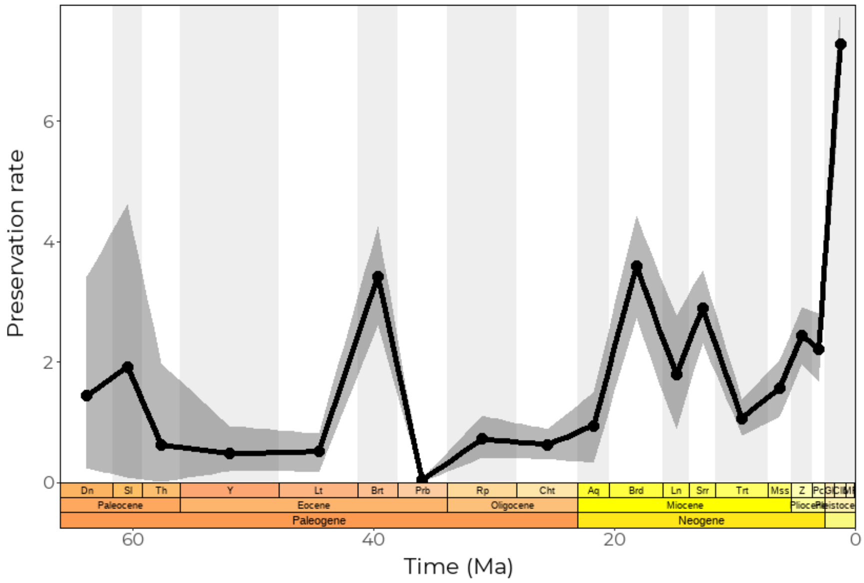
4. Diversity (SQS with grid-cell rarefaction)

This is the sqs (q=0.4) diversity with grid-cell rarefaction (GCR) applied. The curve shows similarity to that of the diversity without GCR, except in the Piacenzian (late Pliocene) where this curve shows a diversity dip.



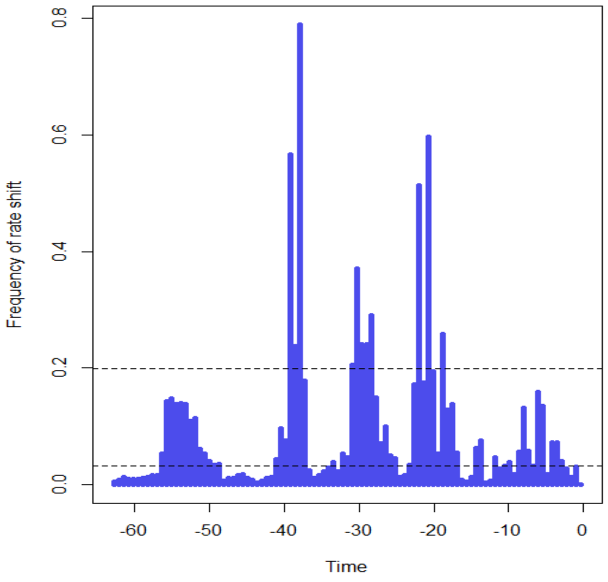
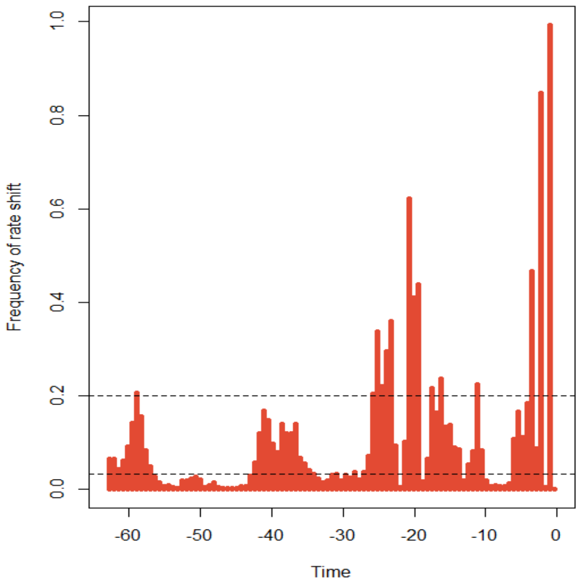
5. Preservation rates

In the following graph I show preservation rates calculated per time bin, using PyRate.



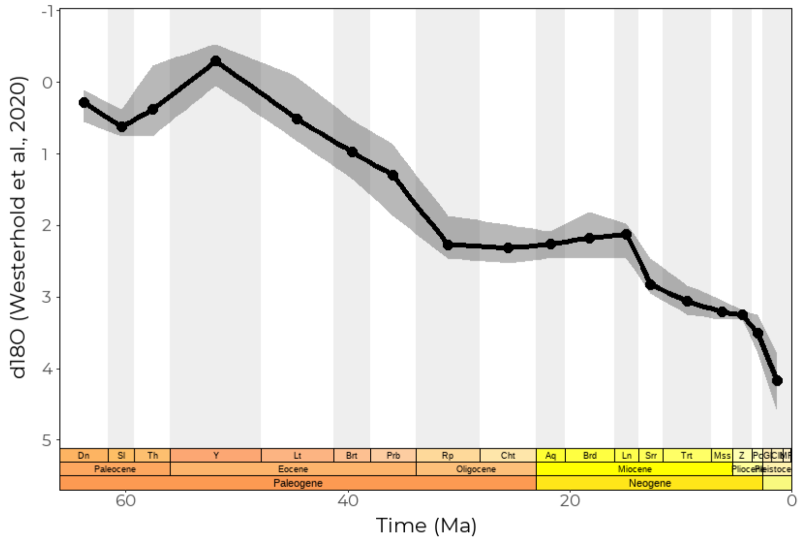
6. Diversification rates with PyRate

The histograms (frequencies) show the calculated times of rate shifts and calculate Bayes Factors in order to determine if the time of a rate shift is supported by a significant posterior probability. Positive evidence of rate shift is when logBF > 2 (lower dashed line) and strong evidence of rate shift is when logBF > 6 (higher dashed line).

Speciation rate shift importance	Extinction rate shift importance
 	

7. Westerhold mean-per-timebin global curve

Palaeotemperature curve, based on the δ^{18}O data from Westerhold et al., (2020). The grey area shows the maximum and minimum mean temperature range of each time bin.

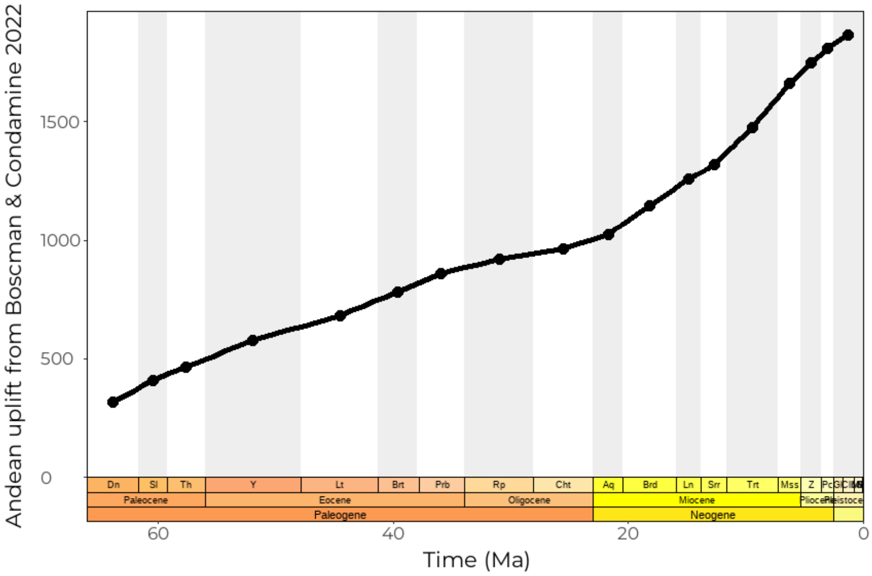


I tested the correlation of these palaeotemperature data with (non-GCR) eutherian diversity. There is not a statistically significant correlation between the global palaeotemperature d18O proxy (Westerhold et al., 2020) and eutherian diversity in South America (slope = 0.670, p = 0.429). This could suggest more local/regional environmental drivers exist.

	Slope (Estimate)
δ^{18}O	0.670 ($p = 0.429$)
Intercept Estimate	Adjusted R squared
12.702 ($p > 0.001$)	-0.024 ($p = 0.429$)

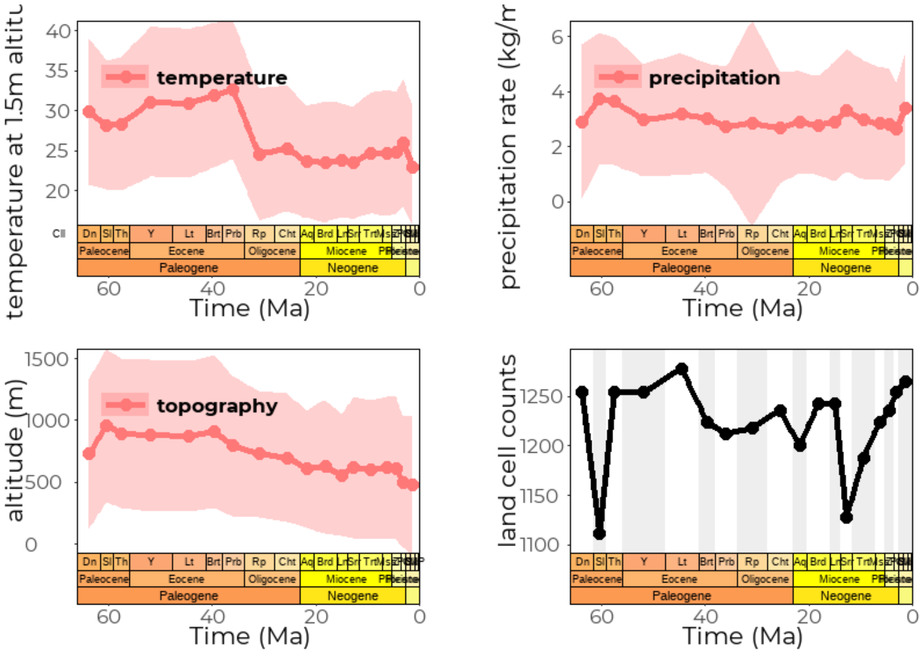
8. Andean uplift

The following graph shows the mean values (in m) of Andean uplift per time bin.



9. South American continent palaeoclimatic variable curves (Getech stage-level from HadCM3)

Mean temperature, precipitation, topography (altitude in m), and number of land cells per time bin, for South America. These data come from the HadCM3 models.



I calculated the regression between South American continent palaeoenvironmental variables & SQS diversity without GCR. There is no statistically significant correlation between temperature, precipitation and topography on eutherian diversity in South America.

	Slope (Estimate)
Temperature	-0.973 (p = 0.095)
Precipitation	0.714 (p = 0.871)
Topography	0.018 (p = 0.217)
Intercept Estimate	Adjusted R squared
25.709 (p = 0.126)	0.052 (p = 0.337)

10. Individual eutherian group diversity curves & regression with whole-eutherian curve (non GCR)

Performed a general least-square regression (GLS) to test the effect of caviomorph, xenarthran and SANU diversity curves on full eutherian curve (non GCR).

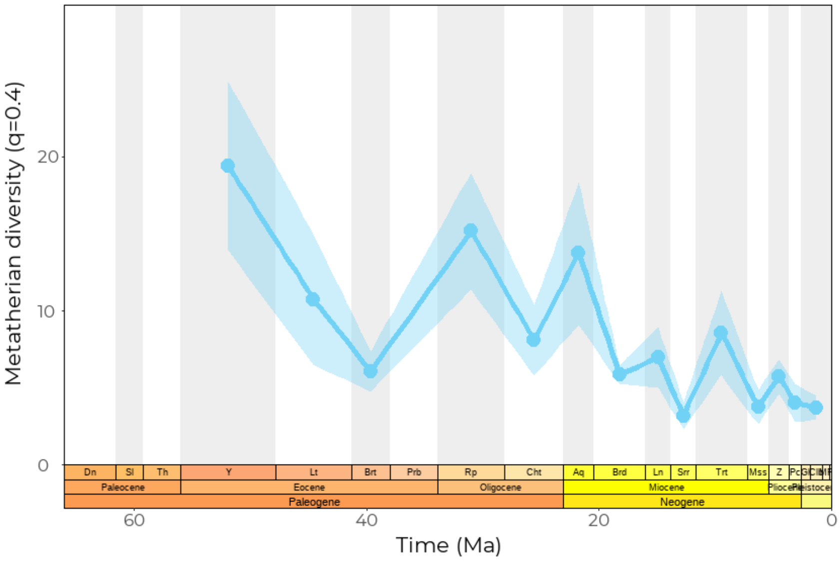
	Number of unique genera
caviomorphs	336
xenarthrans	390
SANU	386

All groups were found to significantly and positively drive the all-eutherian diversity curve. Xenarthrans have the biggest effect (slope = 1.026) followed by caviomorphs (slope = 0.944) and SANU (slope = 0.868).

	Slope (Estimate)
caviomorphs	0.944 (p = 0.036)
xenarthrans	1.025 (p > 0.002)
SANUs	0.868 (p = 0.008)
Intercept Estimate	Adjusted R squared
4.097 (p = 0.267)	0.879 (p = 0.001)

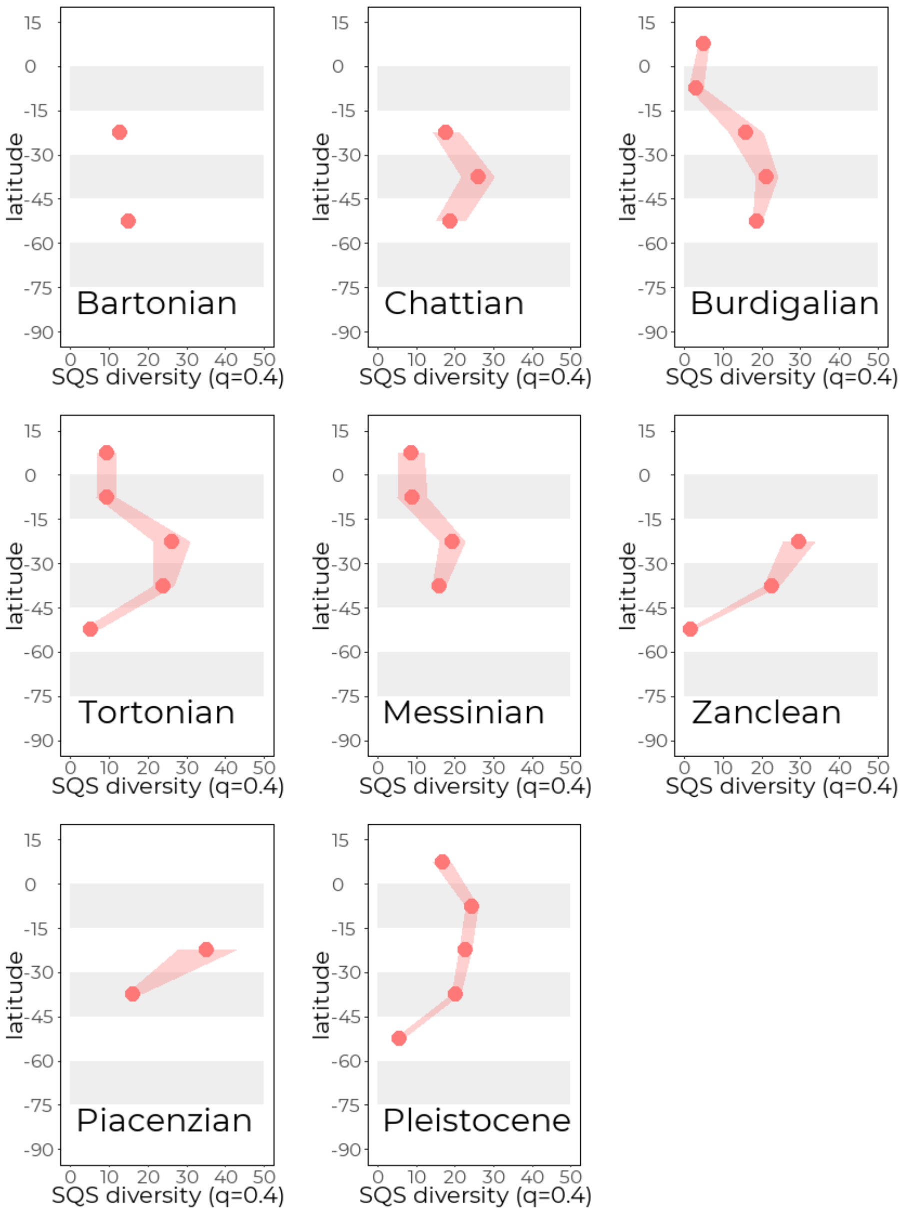
11.Metatherian diversity (without GCR)

I calculated the SQS diversity of metatherians, in the same way as in eutherians in this thesis.



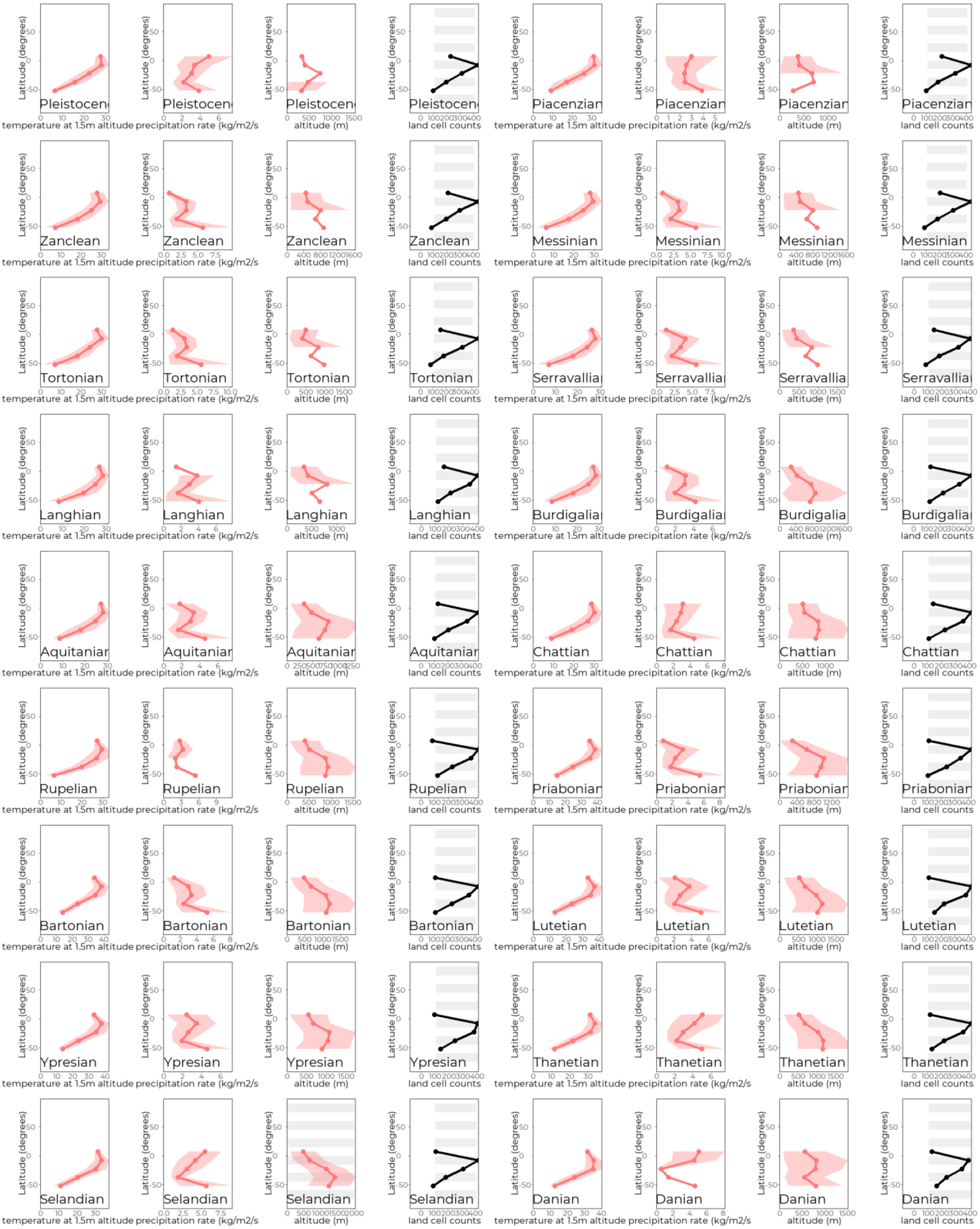
12. Latitudinal SQS diversity for specific time periods

The following graphs were produced, for periods with enough data that could produce more than one point.



13. Palaeoenvironmental variables in latitude

I also calculated the HadCM3 modelled palaeoenvironmental variables mean (faded area consists of maximum and minimum values for each bin).


Latitude (degrees)
Pleistocen
temperature at 1.5m altitude
Pleistocen
precipitation rate (kg/m2/s
Pleistocen
altitude (m)
Pleistocen
land cell counts
Piacenzian
temperature at 1.5m altitude
Piacenzian
precipitation rate (kg/m2/s
Piacenzian
altitude (m)
Piacenzian
land cell counts
Zanclean
Zanclean
Zanclean
Zanclean
Messinian
Messinian
Messinian
Messinian
Tortonian
Tortonian
Tortonian
Tortonian
Serravallia
Serravallia
Serravallia
Serravallia
Langhian
Langhian
Langhian
Langhian
Burdigalia
Burdigalia
Burdigalia
Burdigalia
Aquitaniar
Aquitaniar
Aquitaniar
Aquitaniar
Chattian
Chattian
Chattian
Chattian
Rupelian
Rupelian
Rupelian
Rupelian
Priabonian
Priabonian
Priabonian
Priabonian
Bartonian
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Lutetian
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Lutetian
Ypresian
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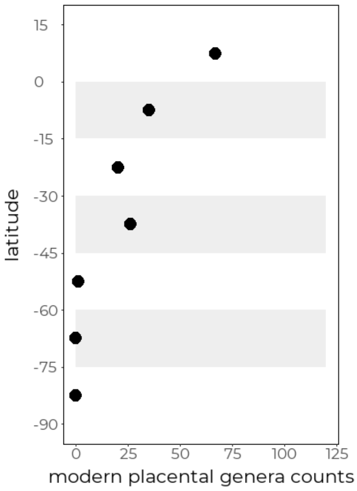
Danian

I calculated a regression of spatial palaeoenvironmental variables and eutherian diversity (non GCR). Analyses either didn't have a large enough sample size, or showed a non-significant effect of palaeoenvironmental variables on eutherian diversity latitudinally. The exception is the Pleistocene, where latitudinal distribution of temperature (slope = 0.765, p = 0.015) and most importantly precipitation (slope = -4.329, p = 0.027) significantly drive eutherian diversity.

	Slope (Estimate)
Temperature	0.765 (p = 0.015)
Precipitation	-4.329 (p = 0.027)
Topography	0.004 (p = 0.0.152)
Intercept Estimate	Adjusted R squared
15.592 (p = 0.037)	0.998 (p = 0.025)

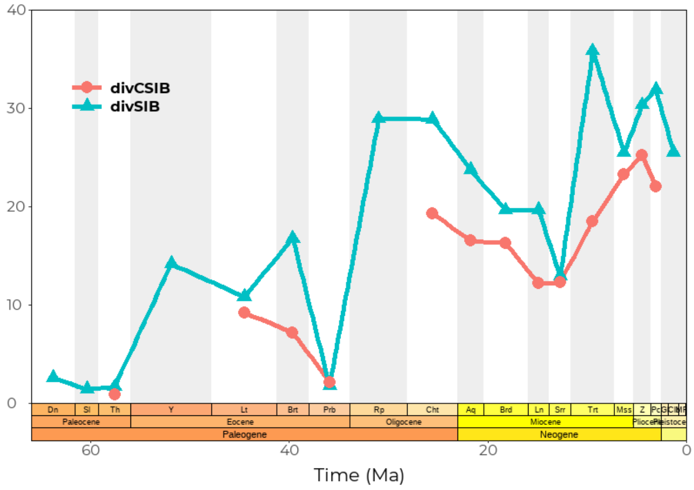
14.Raw counts of modern South American placentals per latitude

I calculated the raw counts of unique general of extant South American placentals for each latitudinal bin, based on data from GBIF.

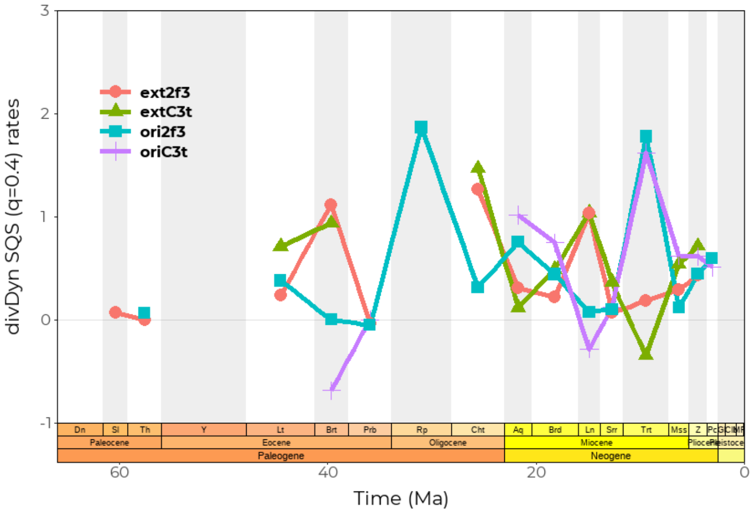


15.Diversification rates (SQS without GCR)

I calculated sampled-in-bin (SIB) and corrected SIB (CSIB) diversification rates by time bin (Alroy, 2008) using the divDyn package in R.

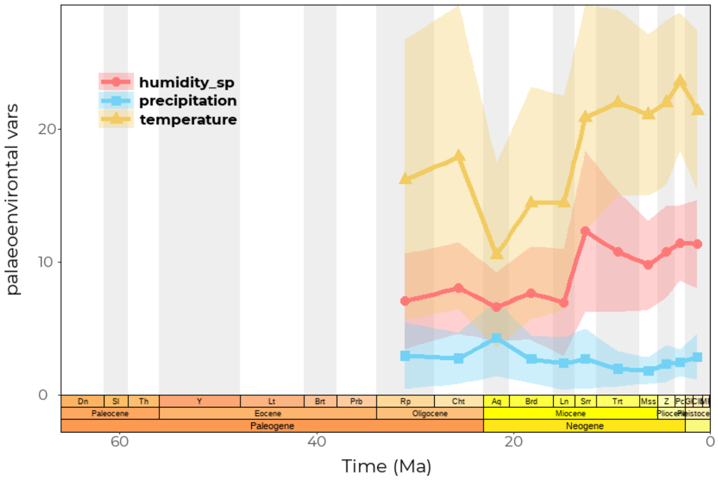


Similarly, I calculated the following origination and extinction rates per time bin: second-for-third (2f3) rates (Alroy, 2015) and corrected three-timer (C3t) rates (Alroy, 2008).



16.Occurrence-based palaeoclimatic variable curves

I have calculated palaeoenvironmental variables per time bin. These are the mean values (faded area is restricted by the maximum and minimum value in each time bin) of each variable, calculated taking into account only cells that contain fossil occurrences used in this thesis.



I performed a regression between these occurrence-based palaeoenvironmental variables & SQS diversity without GCR. The regression results show that temperature (slope = 1.166, p < 0.001) and humidity (slope = -2.45, p < 0.001) drive South American eutherian diversity.

	Slope (Estimate)
Temperature	0.804 (p = 0.432
Precipitation	0.994 (p = 0.755)
Topography	-1.584 (p = 0.336)
Intercept Estimate	Adjusted R squared
12.115 (p = 0.434)	-0.228 (p = 0.770)

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