



Reconstructing Cenozoic Patagonian biotas using multi-proxy fossil records

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ARTICLE INFO

Keywords:

Patagonia
Fossil record
Cenozoic
Ecosystems

ABSTRACT

The fossil record from Cenozoic sediments provides a great deal of information that has direct bearing on the early assembling of modern Patagonian ecosystems. In this synthesis, we revise selected fossil marine and terrestrial records from the last 66 Ma with the aim of understanding major shifts of Patagonian biotas. From the Paleocene to the mid Eocene this region supported outstandingly diverse terrestrial assemblages that show strong connections to modern-day Australasia (e.g. gum trees, casuarinas, monotremes). Nearshore marine biotas confirm peak warmth conditions, with tropical species with Tethyan affinities. The late Eocene and early Oligocene marks the onset of a period of overall regional cooling, drying, and increasingly variable ecological conditions. The rise of palm-dominated flammable biomes in hinterlands and the prevalence of Gondwanan gallery forest (e.g. southern beeches and podocarps) along river-sides supported the existence of mosaic habitats maintained by edaphic and regional climatic conditions. This shift in landscapes reflects the evolution of a wide range of herbivorous mammals (e.g. Notoungulata, Litopterna, and Astrapotheria). The late Oligocene and early-to-mid Miocene witnessed a dramatic modification of landscapes including the incursion of high sea-level episodes, the emergence of specialized coastal (i.e. salt-marsh) plant taxa and the expansion of large herbivorous mammals with predominantly high-crowned teeth (e.g. Notoungulata: Hegetotheriidae, Interatheriidae, and Mesotheriidae). The cooling trend of this interval was interrupted by a mid-Miocene transient warming event, with the dispersion of terrestrial (e.g. platyrrhine monkeys, palms) and marine (e.g. *Tuberculodinium vancampoeae*) elements with tropical affinity into southernmost South American regions. Seasonally-dry conditions increased towards the end of the Miocene, yet subtropical species persisted either in terrestrial (e.g. malpighs, passion vines, capybaras), and marine (e.g. Subtropical and Caribbean molluscs) environments. The increasing aridity caused by the Andean uplift wiped out most of the forest species and promoted the diversification of open-habitat species; the emergence of the current grass-dominated Patagonian Steppe occurred later on, probably during the Quaternary.

1. Introduction

The word Cenozoic (originally Kainozoic) comes from the Greek

word *Καινός*, meaning ‘recent life’, and represents the last 66 Ma of Earth history. During this Era, flowering plants and mammals –among the most prominent examples– began to rule terrestrial ecosystems,

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<https://doi.org/10.1016/j.jsames.2021.103513>

Received 3 June 2021; Received in revised form 5 August 2021; Accepted 6 August 2021

Available online 14 August 2021

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following the collapse of gymnosperms and the extinction of non-avian dinosaurs at the end of the Cretaceous. The opening of the Drake Passage or 'Mar de Hoces' (between South America and Antarctica) and the onset of the Antarctic Circumpolar Current led to one of the most important paleoclimatic reorganizations of the Cenozoic in the Southern Hemisphere. These events, along with the gradual uplift of the longest South American mountain chain (the Andes), marked a continuous modernization of landscapes and ecosystems. In Patagonia, more particularly, such modernization is evidenced by numerous large-scale extinction events and high ecological turnover phases; for example, biotas with predominantly Neotropical, Gondwanan, Weddellian, or Australasian distribution became strongly reduced or extinct across the Paleogene (e.g. *Gymnostoma* and *Eucalyptus*, among plants, and gondwanatheres, monotremes, polidolopid metatherians and some archaic ungulates among mammals) while more modern biotas with typical austral distribution –including species with clear adaptations to aridity– rose to prominence during the Neogene (e.g. grasses, daisies, and guanacos). These and other landscape-level biotic shifts can potentially be traced by studying the Patagonian fossil record. Over the course of at least the last 130 Ma (Vizcaíno et al., 2013) many thousands of well-preserved fossil faunal and floral remains have been recorded from Cenozoic terrestrial and marine deposits from Patagonia, providing a unique record of life in deep time across this austral region.

The geographic distributions of plant and animal species, as well as communities, are greatly influenced by many abiotic factors, among them the climate. There are many published studies from Patagonia that inferred paleoclimatic conditions based on paleontological data. For example, the climatic preferences of the nearest living relatives of a fossil taxon have been used to demonstrate that during the mid-Miocene, Patagonia was at least warmer and wetter than today because of the occurrence of remains unambiguously assigned to New World monkeys (platyrrhines) and pollen grains and phytoliths assigned to palms (Arecaceae) (Dunn et al., 2015; Kay et al., 2021; Barreda and Palazzesi, 2021; but see the discussion on the uncritical use of this criterion in Kay et al., 2021). Similarly, sea surface temperatures were considerably higher than those of today at sub-Antarctic latitudes because of the high occurrence of late Miocene shells (e.g. *Amusium*, *Nodipecten*) and dinoflagellate cysts (e.g. *Tuberculodinium vancampoe*) with largely tropical modern distribution (Guler et al., 2021; del Río, 2021). Many of the published climatic and ecological reconstructions from Patagonia have been undertaken mostly on the basis of major terrestrial taxonomic groups, either qualitatively (e.g. plants, Palazzesi and Barreda, 2007; mammals, Woodburne et al., 2014) or quantitatively (e.g. plants, Wilf et al., 2003; Palazzesi et al., 2014; Ruiz et al., 2021; mammals, Kay et al., 2021). Here we review terrestrial and marine fossil records of selected plants and animals with the aim of providing a more complete picture of how ecosystems responded to the major climatic events of the last 66 Ma.

The Patagonian fossil record is inherently patchy and discontinuous, and there are definitely large gaps because bearing rocks are either eroded or barren, particularly during parts of the Paleocene, Eocene, and Pliocene. Although this can potentially distort terrestrial and marine reconstructions, most key climatic events across the Cenozoic are largely represented in Patagonia. Using the vast Cenozoic Patagonian stratigraphic and fossil record, here we aim to review 1) the timing of major marine flooding events; 2) the phases of warming and cooling trends; 3) the replacement of communities with contrasting biogeographical histories; 4) the major shifts of terrestrial landscapes; and 5) the key biotic events that led to the modernization of the Patagonian landscapes. Combining our understanding of the fossil record derived from terrestrial and marine environments, we provide a more accurate scene of how Patagonian ecosystems assembled across the Cenozoic Era.

2. Methods

We review selected terrestrial and marine records from the Cenozoic

of Patagonia in light of the major fossil discoveries and regional geochronological studies. Patagonia occupies the southernmost region of South America both in Chile and Argentina (Fig. 1); in this synthesis we select records from the Argentine provinces Neuquén, Río Negro, Chubut, Santa Cruz, and Tierra del Fuego. Fossil-bearing deposits are not evenly distributed through the Cenozoic in Patagonia, and most of them derived either from marine sediments accumulated by episodes of relative sea level rise or by terrestrial sediments deposited by fluvial and loess sedimentation; here we organize the results of our overview following the Cenozoic Epochs, and we begin each one with earliest available record, either terrestrial or marine. The geochronology of the South American Land Mammal Ages (or SALMAS) mentioned throughout this contribution and the geographic and temporal distribution of the Cenozoic marine incursions have been shown (Bellosi et al., 2021, Fig. 11; Reguero and Goin, 2021, Fig. 7) and reconstructed and illustrated (e.g. Malumián, 1999; Malumián and Náñez, 2011; Náñez and Malumián, 2019; Scasso et al., 2012; del Río et al., 2013; Guler et al., 2019; Parras and Cuitiño, 2021) elsewhere, respectively.

To further explore the long-term relationship between the paleoclimate and past biotas, we plot estimates of global temperature fluctuation (Fig. 2) and global sea level change (Fig. 3) against some key biotic indicators or events. We extract 0.5 Ma bins from global temperature fluctuation (Westerhold et al., 2020) and global sea level change (Miller et al., 2020) using R package "dplyr" (Wickham et al., 2020) and plotted using R Core Team (2020).

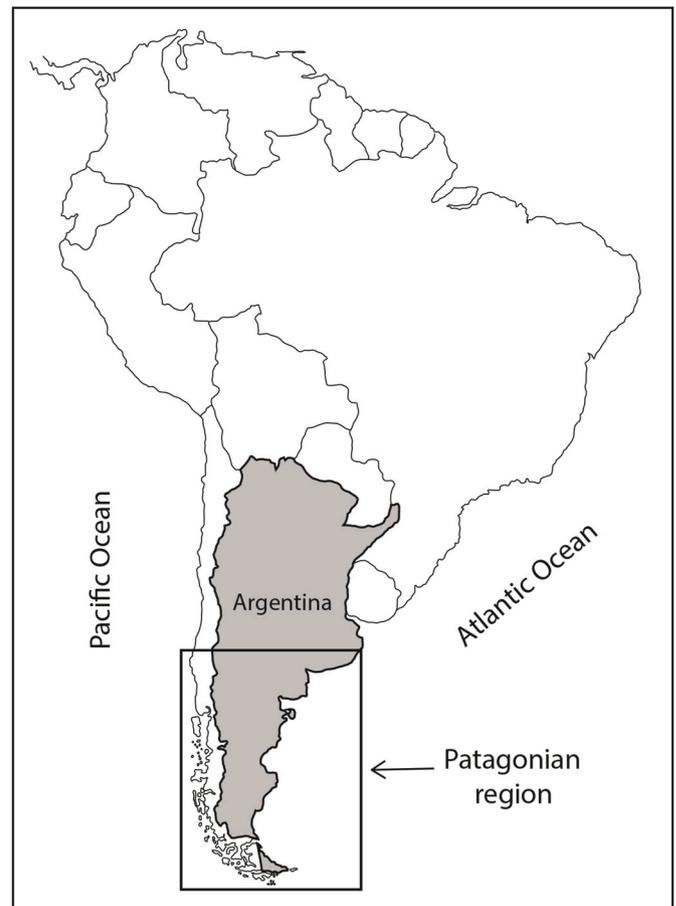


Fig. 1. Map of South American showing the Patagonian region. In this synthesis we selected records preserved in the Neuquén, Río Negro, Chubut, Santa Cruz, and Tierra del Fuego provinces from Argentina.

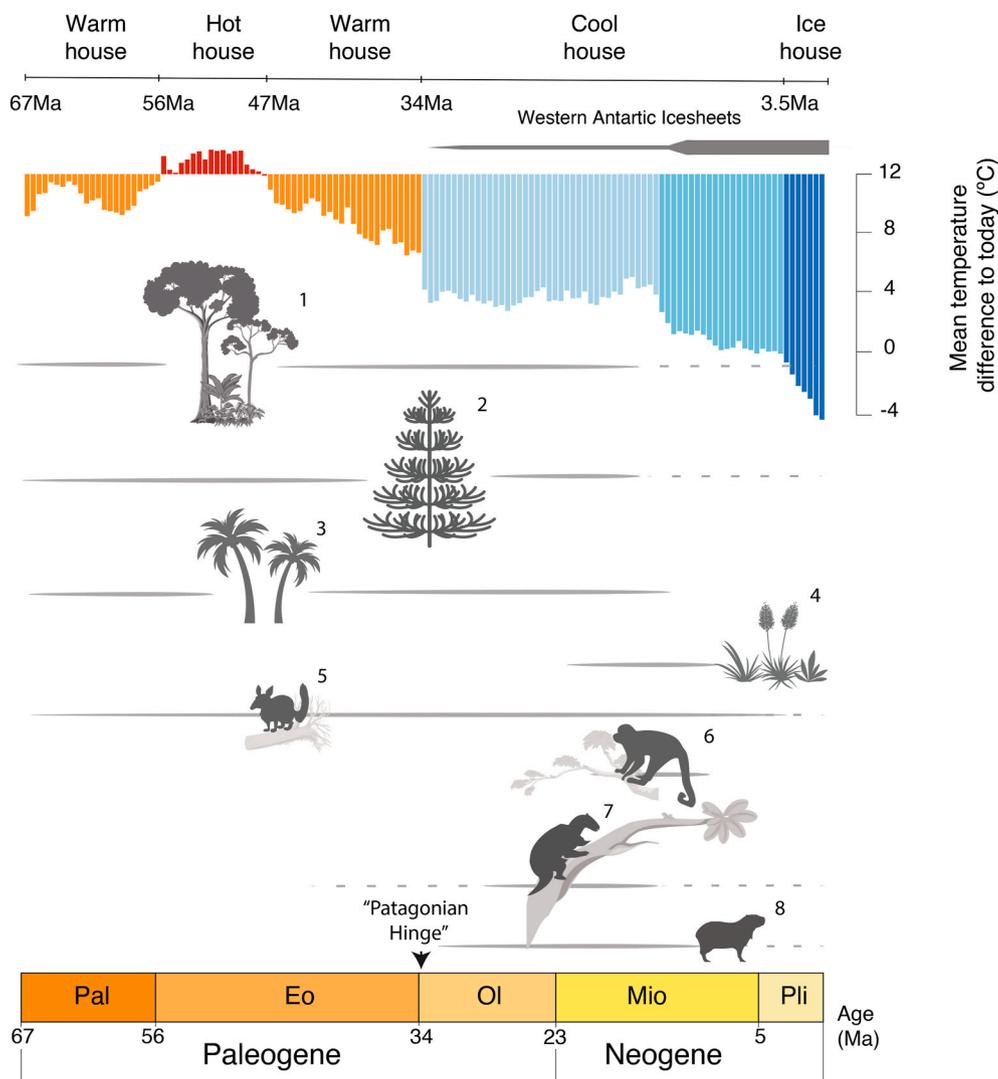


Fig. 2. Cenozoic climatic trends against key terrestrial biotic events from Patagonia. The time histogram with 0.5 Ma bin size represents variations of benthic foraminiferal oxygen Isotope Dataset from ocean drilling cores spanning the past 66 years (West-erhold et al., 2020). The four climatic states (Hothouse, Warmhouse, Coolhouse and Icehouse) reflect greenhouse gas concentrations and polar ice sheet volume. 1- Humid-demanding forests with a fern-dominated understory extended across Patagonia during much of the Paleogene, became fragmentary during the late Eocene and disappeared during the late Miocene from non-Andean regions; 2- Araucariaceae (monkey puzzle family) occurred frequently across Patagonia –even along the coast– until the late Miocene, when it was probably the tallest existing tree; 3- Arecaceae (palms) –one of the most iconic warm-demanding families– occurred continuously across Patagonia until the mid-Miocene, when it became extinct from the region (probably migrating northwards) just after the MCO; 4- Asteraceae (daisies) and other representatives of open-habitats (including salt-marsh species) rose to prominence during the Miocene; 5- Mammal faunas reached their greatest diversity in the early Eocene, including metatherians (e.g. polydolopids); during mid-late Eocene, eutherians include a diverse set of cursorial brachyodont herbivores. 6- Early Miocene mammal communities show open-habitat species coexisting with an increasing number of forest-dwelling elements with many arboreal clades, including the first records of primates in Patagonia. 7- Among other Early Miocene forest indicators sloths were diverse, including from facultative to semi-arboreal folivores. 8- Caviomorph rodents arrived in Patagonia during the latest Eocene or early Oligocene, and by the late Oligocene they were highly diversified; low-crowned browsing porcupines (Erethizontoidea) also indicate the presence of forests during the early Miocene; in the late Miocene of

Península Valdés occurs the southernmost record of a capybara (Caviioidea; Hydrochoeridae) in an inferred warmer and seasonally drier climate than that of today (Dozo et al., 2010). By the middle Miocene the number of arboreal mammal clades declined and euhypsodont notoungulates and rodents became more common, suggesting progressively more open and xeric environments.

3. Results

3.1. Paleocene

During the latest Cretaceous and early Paleocene, large extensions of Patagonia became flooded by the first Cenozoic Atlantic incursion. This transgression is represented by shallow shelf and marginal marine deposits from northern (i.e. Neuquén, Colorado, Cañadón Asfalto, and Valdés), central (i.e. Golfo San Jorge) and southern (i.e. Austral) basins. The Cenozoic flooding event ranges from the early Danian (66 Ma) to the middle Selandian (~60.4 Ma) based on planktic foraminifera, calcareous nannofossils, molluscs, dinoflagellate cysts, ostracods and radiometric data (e.g. Echevarría, 1995; Nañez and Concheyro, 1997; Palamarczuk et al., 2002; del Río et al., 2011; Clyde et al., 2014; Vellekoop et al., 2017; Guler et al., 2018, 2019; Fosdick et al., 2020; González Estebenet et al., 2020, among others). This transgression deposited sediments with abundant fossils (e.g. del Río et al., 2007, 2008, del Río, 2012, 2021; del Río and Martínez, 2015; Vellekoop et al.,

2017; Woelders et al., 2017; Guler et al., 2019; González Estebenet et al., 2020). The retraction of this shallow sea left behind extensive coastal swamps, fluvial, and volcanoclastic deposits that preserved diverse faunas and floras (e.g. Pascual and Ortiz-Jaureguizar, 2007; Goin et al., 2012, in press; Iglesias et al., 2007; Barreda et al., 2012; Ruiz et al., 2017; Donovan et al., 2018; Martínez et al., 2018; Stiles et al., 2020; De Benedetti et al., in press).

Early Paleocene Patagonian dinoflagellate assemblages are commonly dominated by gonyaulacaceans (e.g. *Danea*, *Cordosphaeridium*, *Spiniferites*), areoligeraceans (e.g. *Glaphyrocysta*), and peridiniaceans (e.g. *Senegalinium*). Many typically recognized Late Cretaceous peridinioid dinocysts (e.g. the deflandroid genus *Manumiella*) became extinct in the Early Paleocene, and were replaced by the expansion of other peridinioid genera (e.g. *Senegalium*, *Cerodinium* and *Deflandrea*). Danian dinocyst assemblages from northern Patagonia show high abundances of tropical (Tethyan) species (e.g. *Trithyrodonium evittii*, *Glaphyrocysta* spp.) whereas in southern Patagonia, they record peaks of cool-water species (e.g. *Palaeoperidinium pyrophorum*).

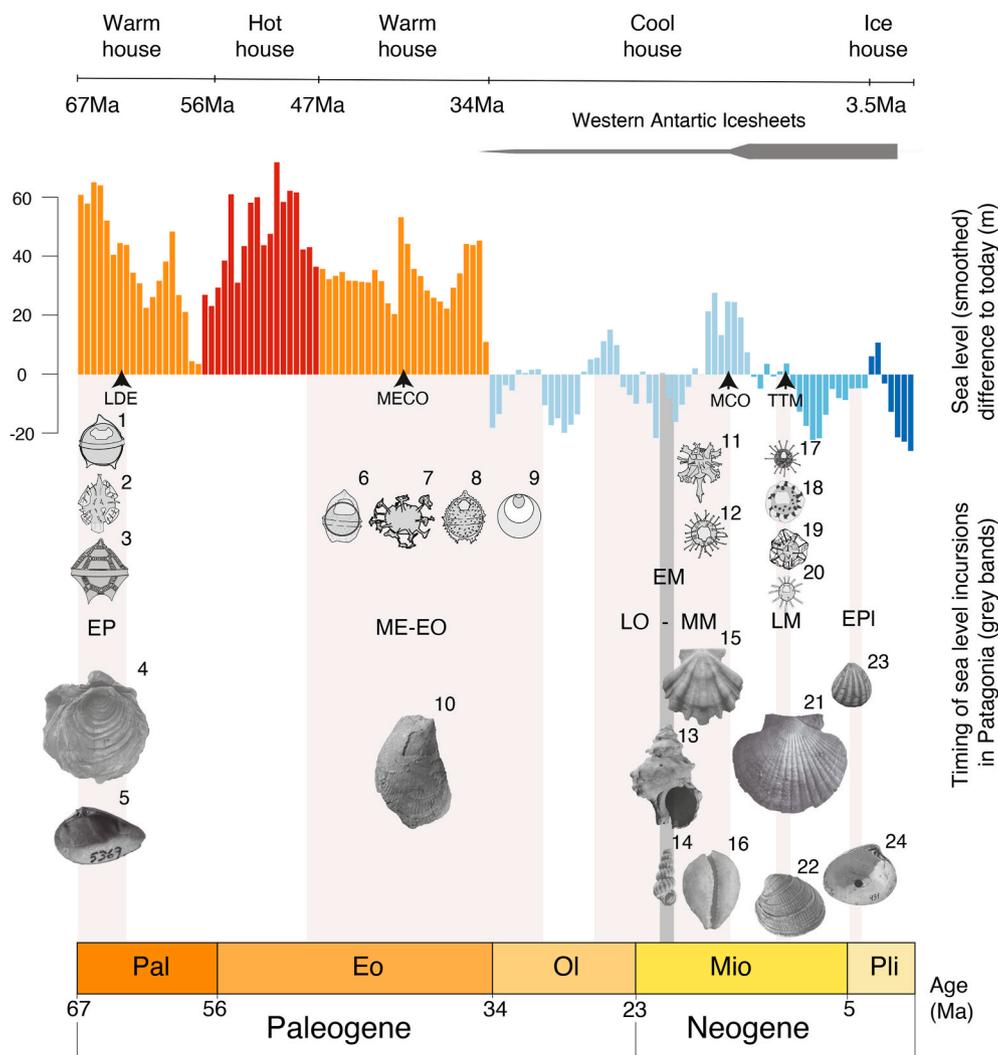


Fig. 3. Cenozoic global mean sea level against key marine taxa from Patagonia. The time histogram with 0.5 Ma bin size represents variations in global mean sea level derived from benthic foraminiferal $\delta^{18}\text{O}$ and Mg/Ca records, spanning the past 66 years (Miller et al., 2020). Successive marine incursions flooded wide areas of Patagonia during the Cenozoic and left behind sediments with a rich fossil record of organic-walled cysts (dinocysts) and molluscan faunas, among other marine elements. Grey bands indicate the timing of those Patagonian transgressions: early Paleocene (EP), middle Eocene-early Oligocene (ME-EO), late Oligocene-middle Miocene (LO-MM), early Miocene maximum flooding event (EM, with a darker grey band), late Miocene (LM) and early Pliocene (EPL). The early Danian thermal transient event (LDE) is recognized in northern Patagonia by the presence of typically Tropical (Tethyan) dinocyst taxa such as *Trithyrodinium evittii* (1) along with other warm-demanding species (e.g. *Damassadinium californicum* (2)). Peaks of the cool-water *Palaeoperidinium pyrophorum* (3) occurred in the middle Danian of southern Patagonia. Similarly, early Danian molluscan assemblages contain Tropical taxa with Tethyan affinities such as *Gryphaostrea* (4) and *Bathytormus* (5), with the addition of Subtropical Southern United States elements (SUS) and Paleoaustral elements. During the Middle Eocene Climatic Optimum (MECO), dinocysts from southern Patagonia include Endemic Antarctic taxa (e.g. *Deflandrea antarctica* (6), and *Vozzhemikovia apertura* (8)) with peak abundances of the warm-water *Enneadocysta dictyostila* (7). Molluscs include virtually the same Danian Subtropical Paleoaustral, SUS and Tropical taxa with Tethyan affinities such as *Acesta (Plicacesta)* (10). During the late Eocene the Endemic Antarctic taxa persisted, with the addition of the cool-water marker *Gelatia inflata* (9), among others, indicating the

shallow opening of the Sea of Hoces (Drake passage). By the late Oligocene-early Miocene, molluscan assemblages show a declining contribution of Tropical and the Subtropical (SUS and Paleoaustral) taxa coupled with the massive rise of the Subtropical Neogene Southern elements (*Sassia* (13), *Cirsotrema* (14)), revealing lower temperatures than those of the Paleogene, yet higher than today. The Miocene Climatic Optimum (MCO) is associated with maximum offshore flooding events, with the presence of outer neritic to oceanic dinocyst assemblages from northern and central Patagonia, including peak abundances of warm-water adapted taxa (e.g. *Hystrichokolpoma rigaudiae* (11), *Dapsilidinium pseudocolligerum* (12), *Melitasphaeridium choanophorum*, *Reticulatosphaera actinocoronata*). The highest common occurrence of these taxa along with the extinction of *Dapsilidinium pseudocolligerum* and *Hystrichokolpoma rigaudiae* are related with cooler sea surface temperatures after the MCO at ~14 Ma. Molluscan faunas include the first major occurrence of Caribbean taxa –represented by *Nodipecten* (15) and *Muracypraea* (16)– in agreement with the MCO conditions. The late Miocene warming event (or Tortonian Thermal Maximum; TTM) records a maximum flooding episode, represented by outer neritic to oceanic dinocyst assemblages with peak abundances of warm-water taxa e.g. *Operculodinium centrocarpum* (17), *Tuberculodinium vancampoe* (18), *Reticulatosphaera actinocoronata* (19), *Melitasphaeridium choanophorum* (20). Molluscs reveal Subtropical conditions with the occurrence of new Caribbean taxa such as *Leopecten* (21) and *Chionopsis* (22). Early Pliocene faunas lack Caribbean elements that may have retracted northwards, to lower latitudes. Except for a few genera (i.e. *Kolmeris* (23), that did not persist in the Southwestern Atlantic Ocean, most of the Pliocene taxa survived until Recent times (*Eucallista* (24).

Molluscan assemblages mainly include Cosmopolitan genera, although the presence of tropical (or Tethyan; e.g. *Bathytormus*, *Acesta (Plicacesta)*, and *Gryphaostrea*), subtropical (or southern United States taxa; e.g. *Tejonina*, *Heterotermia*, *Yoldia (Calorhadia)*, as well as Paleoaustral taxa (e.g. *Neilo*, *Pteromyrtea*, *Austrophaera*, *Struthioptera*, *Priscaphander*) provide a distinctive signature to this fauna (del Río, 2021). Endemic genera include *Rocalaria*, *Austrophaera*, and *Pseudotylostoma*, among others.

Floras from the early Paleocene preserve diverse assemblages including Australian rainforest endemics (e.g. Akaniaceae, Casuarinaceae) as well as Neotropical elements (e.g. Sapindaceae, Arecaceae,

Menispermaceae). Legumes (Fabaceae) are represented by one of the oldest records (Brea et al., 2008). Gymnosperms of Gondwanan affinity (e.g. podocarps and araucarias) were abundant as well as the fossil genus *Classopollis* (Cheirolepidiaceae). Nothofagaceae (southern beeches), although present, were very scarce. Ferns were also abundant and diverse (e.g. *Lygodium*, *Dicksonia*).

The oldest Paleocene mammalian faunas in Patagonia retain the Gondwanan (“West Weddellian”) non-tribosphenic lineages (e.g. Gondwanatheria, Dryolestida and Monotremata), several derived Metatheria (e.g. Polydolopimorphia and “Ameridelphians”), and several

South American Native Ungulates (or SANUs; e.g. Notonychopidae and Didolodontidae). Eutherians are represented by the notonychopid *Requisia vidmari*, the oldest known litoptern (Bonaparte and Morales, 1997). Late Paleocene faunas include large SANUs such as the xenungulates *Carodnia* and *Notoetayoa* (Gelfo et al., 2008). Paleocene herbivorous mammals, except for the gondwanatherian *Sudamerica ameghinoi*, bear a wide range of brachyodont cheek teeth, interpreted to have been mostly insectivorous, frugivorous or folivorous. The hypsodonty of gondwanatherian mammals is probably related to nutritional needs that included abrasive components (Koenigswald et al., 1999; Woodburne et al., 2014).

3.2. Eocene

Early Eocene sedimentation includes restricted regions with caldera-lake systems (for geographic and stratigraphic details see Gosses et al., 2021) that preserved diverse floras (e.g. Romero and Hickey, 1976; Gandolfo et al., 1988, 2011; Gandolfo and Hermsen, 2017; Wilf et al., 2005, 2009; Wilf, 2012; Zamalao et al., 2006, 2020; Jud et al., 2018). Mid-late Eocene Atlantic incursions recorded mainly in southern Patagonia include shallow marine and highly fossiliferous sediments that have been constrained to the middle to late Eocene ages (Griffin, 1991; Malumián and Caramés, 1997, 2000a; Camacho et al., 1998, 2000a, b; Malumián, 1999; Olivero and Malumián, 1999; Olivero et al., 2020; Guerstein and Junciel, 2001; Guerstein et al., 2014; Casadío et al., 2009; González Estebenet et al., 2016; del Río, 2021). Recently, U–Pb geochronological results constrained the onset of this flooding event at ~47 Ma (Fosdick et al., 2020). Although geographically restricted, this marine episode preserved abundant terrestrial fossil remains (e.g. Romero, 1977; Vento et al., 2016; Panti, 2019; Pujana and Ruiz, 2019; Fernández et al., 2021). Coeval emerged lands from hinterland include extensive pyroclastic, loessic, and fluvial sedimentation, with rich faunas (e.g. Madden et al., 2010 (and chapters therein); Reguero and Prevosti, 2010; Kramarz et al., 2011).

Early Eocene Patagonian terrestrial floras are among the most diverse assemblages known worldwide, with taxa occurring today in tropical to southern-temperate rainforests from Australasia such as *Papuacedrus* (Cupressaceae), *Agathis* (Araucariaceae), Akaniaceae, Schizomeriaceae (Cunoniaceae), *Ceratopetalum* (Cunoniaceae), *Eucalyptus* (Myrtaceae), and *Gymnostoma* (Casuarinaceae). By mid-Eocene times, most of them became extinct or highly reduced. The widespread retraction of Australasian elements mirrored a massive expansion of southern beeches (Nothofagaceae) along with other canopy Gondwanan conifers (mainly podocarps and araucarias) (Barreda et al., 2021; Gandolfo and Zamalao, 2021). However, neotropical elements still occurred frequently (e.g. Arecaceae and Malpighiaceae).

Land mammal faunas reached their greatest diversity in the early Eocene, largely including small insectivorous (e.g. “Ameridelphians”), omnivorous (e.g. protodidelphids) and browsing (e.g. gashterniids) mammals. Early-mid Eocene faunas include a great diversity of metatherians and eutherians, and the last gondwanatherian mammals from South America (Goin et al., 2012b). This fauna shows an evident southern connection (West Weddellian) with Antarctica, including the presence of derorhynchid metatherians and litoptern eutherians (e.g., Sparnotheriodontidae, *Sparnotheriodon* in Patagonia and *Notiolofos* in Antarctic Peninsula). These litopterns along with other mid-Eocene herbivorous notungulates (isotemnids, i.e. *Thomashuxleya*) with relatively large-bodies, exhibit dentition with adaptations for browsing and grasping low vegetation (Croft, 2016). During mid-late Eocene, eutherians show a high diversity (e.g. xenarthrans, notungulates, litopterns), while metatherians still occurred (polydolopids), supporting the interpretation of a diverse set of cursorial herbivore niches, clearly dominated by brachyodont mammals. During the late Eocene-early Oligocene mammal faunas include a great representation of carnivorous metatherians as well as polydolopimorphs, while xenarthrans declined. By late Eocene, mammal assemblages were still dominated by

brachyodonts; medium size, low crowned and lophodont notungulates (e.g. *Oldfieldthomasia*) probably fed on leaves, twigs and buds (Croft, 2016). The notungulates Archaeohyracidae exhibit slightly more pronounced hypsodonty than its earlier (Casamayoran) counterparts (Reguero and Prevosti, 2010). Large herbivores such as the astrapothere *Astraponotus* (Kramarz et al., 2011) had lower incisors showing probable adaptations for processing of abrasive food items.

Mid and late Eocene marine dinocyst assemblages became largely dominated by Endemic Antarctic taxa (e.g. *Deflandrea antarctica*, *Vozzhennikovia apertura*, *Enneadocysta dictyostila*), referred to as “Trans-antarctic Flora” (Wrenn and Beckman, 1982). This suite of taxa –common to coeval sediments in Australia, Tasman Plateau and Antarctica– exhibits peak abundances of the warm-water dinocyst *Enneadocysta dictyostila* (González Estebenet et al., 2016; Fernández et al., 2021). Towards the end of the Eocene, these Endemic Antarctic elements prevailed, along with the presence of the cool water species *Gelatia inflata* and the increase of the Protoperidiniaceans (Guerstein et al., 2010). Peaks of cosmopolitan species (e.g. *Turbiosphaera filosa*, *Operculodinium* spp.) occurred towards the Late Eocene, although the magnitude of this increase largely depends on the latitude of the sampled sections (González Estebenet et al., 2014).

Molluscan assemblages from the middle Eocene became less diverse when compared with those of the Danian. The number of endemic elements increased, with a new suite of taxa, including *Neovenericor*, *Ameghinomya*, *Adelfia*, *Austrocallista*, *Valdesia* and *Fagnanoa*. Some of the tropical and subtropical Danian taxa (Paleoaustral, Tethyan and Southern United States elements) persisted, with new Tethyan occurrences such as *Solen* (*Eosolen*) and *Electroma* (del Río, 2021).

3.3. Oligocene

Early Oligocene terrestrial sedimentation includes extensive accumulation of volcanic ash and tephric loess across central Patagonia driven by the intense explosive volcanism (Bellosi, 2010), preserving abundant mammalian faunas (e.g. Goin et al., 2010). Fluvial sediments with carbonaceous sandstones in southern Patagonia contained some floras (e.g. Olivero et al., 1998; Panti et al., 2008; Selkin et al., 2015). Marine sedimentation is confined to the late Oligocene and restricted mostly to the Austral Basin. It is represented by shallow and marginal marine and deep marine deposits (Parras and Cutiño, 2021). The timing of this flooding event in southern Patagonia using ⁸⁷Sr/⁸⁶Sr indicated ages between 25.3 and 22.7 Ma (Chattian-earliest Aquitanian; Parras et al., 2008, 2012).

Early Oligocene terrestrial floras predominantly include forests dominated by Gondwanan families (e.g. Nothofagaceae, Proteaceae, and Podocarpaceae) and abundant ferns (e.g. Dicksoniaceae, and Cyatheaceae) in Patagonia’s southernmost regions (Barreda et al., 2021). Coeval floras, growing northwards, include fire-prone communities with frequent palms, and other open landscape species (Selkin et al., 2015) although grasses remained very uncommon. Late Oligocene coastal floras also denote the presence Gondwanan tree-canopy families (e.g. podocarps, araucarias), as well as palms and salt-marsh shrubs (e.g. Amaranthaceae, Ephedraceae) (Barreda, 1997; Barreda and Palmarczuk, 2000a; Nañez et al., 2009).

Earliest Oligocene mammal faunas attests a major radiation of hypsodont notungulates (Croft et al., 2008). The evolution of the first protohypsodont (argyrolagoid) mathatherians and the first glyptodont xenarthran also indicates important faunistic shifts (Shockey and Anaya, 2011). Rodent-like polydolopimorphs, such as the large frugivorous-insectivorous *Kramadolops*, diversified by these times. From early to late Oligocene times, mammal assemblages reveal an increasing trend towards hypsodonty with records of several high-crowned protohypsodont teeth mammals notungulates (e.g. nothippids, toxodontids, archaeohyracids and mesotheriids). Intertheriids and hegetotheriids include all euhippsodont forms. Faunas also experienced an increasing body size; astrapotheres reached giant sizes and exhibited

somewhat higher crown teeth and marked adaptations to abrasive diets than their previous counterparts. The megaherbivore niche is shared with the giant pyrothere *Pyrotherium*, with brachyodont cheek teeth (Kramarz et al., 2011).

Late Oligocene dinocyst assemblages contain scarce records of the Gonyaulacoids (e.g. *Operculodinium placitum*, *Reticulatosphaera actinocoronata*) and Protoperidiniaceans (e.g. *Selenopemphix*, *Brigantedinium*, and *Lejeunecysta*). The warm-water indicator *Tuberculodinium vancampoe* is abundant at some levels (Barreda and Palamarczuk, 2000a). Molluscs include poorly diverse assemblages restricted to southern Patagonia, with *Zygochlamys geminata*, *Crassostrea hatcheri*, “*Turritella*” *ambulacrum*, *Trophon sowerby* and *Perissodonta ameghinoi*, among the most abundant.

3.4. Miocene

A large marine incursion occurred in Patagonia during the early-to-middle Miocene (~22–15 Ma, Parras and Cuitiño, 2021), characterized mostly by shallow marine and marginal marine deposits with abundant fossils (e.g. del Río and Camacho, 1998; del Río, 2004a–b, 2006; Barreda and Palamarczuk, 2000b; Casadó and Griffin, 2009; Nañez et al., 2009; Reichler, 2010). This widespread incursion constitutes a cycle of relative sea-level fluctuations, with a maximum flooding at ~20–19 Ma (Parras and Cuitiño, 2021); this episode preserved abundant marine and terrestrial records (e.g. del Río, 1990, 2021; Palamarczuk and Barreda, 1998; Barreda and Palamarczuk, 2000b; Barreda et al., 2021; Zamalao and Tell, 2005; Fuentes et al., 2019; Parras et al., 2020; Guler et al., 2021). Terrestrial sedimentation includes well exposed sedimentary successions –largely fluvial with high volcanic supply– with abundant and diverse fossils (Vizcaíno et al., 2012; Kay et al., 2021). A younger marine incursion at northern Patagonia occurred during the late Miocene (~10 Ma), represented by shallow marine deposits that preserve exceptionally abundant molluscan faunas (del Río, 1992, 1994). The timing of this event is constrained between 11.9 and 6 Ma (latest Serravalian–Messinian) based on Sr-isotope stratigraphy (Scasso et al., 2001; Palazzesi et al., 2014; del Río et al., 2018).

Miocene dinocyst assemblages predominantly include gonyaulacoid species, represented by the widely distributed genera *Spiniferites* and *Operculodinium*. Protoperidiniacean dinocysts are represented by species of *Lejeunecysta*, *Brigantedinium* and *Selenopemphix*. In early to middle Miocene sediments from central and northern Patagonia, a highly diverse outer neritic to oceanic dinocyst assemblages occurred, with peak abundance of the thermophilic taxa (e.g. *Melitasphaeridium choanophorum*, *Reticulatosphaera actinocoronata*, *Dapsilidinium pseudocolligerum*, *Hystrichokolpoma rigaudiae*) (e.g. Palamarczuk and Barreda, 1998; Guler et al., 2021). By the late Miocene in northern Patagonia, dinocyst assemblages also show significant increase of warm water taxa (e.g. *Tuberculodinium vancampoe*, *Reticulatosphaera actinocoronata*, *Melitasphaeridium choanophorum*) (Fuentes et al., 2019; Guler et al., 2021). Upwards, dinocyst assemblages became less abundant and poorly diverse, and largely replaced by acritarchs (micrhystridid), phrasinophycean (tasmanitids) and/or chlorococcalean algae (*Botryococcus* and *Pediastrum*) in response to a regional shallowing of the southwestern Atlantic basins towards the end of the Miocene.

Early Miocene molluscan assemblages in central and southern Patagonia document the extinction of most of the Paleogene tropical taxa (Tethyan and Southern United States elements). Among the Cosmopolitan elements, the first records of genera distributed in tropical and subtropical regions (*Crassatella*, *Ficus*, *Conus*, *Dalium*) occurred. Paleogene Subtropical and Paleoaustrian taxa became mostly replaced by a massive occurrence of other Subtropical genera [Southern Neogene elements] such as *Neopanias*, *Cirsotrema*, *Penion*, *Kaitoa*, *Xymene*, and *Sassia*, among the most abundant. Towards the middle Miocene, molluscan faunas underwent a marked decrease of the Southern Neogene elements. A new increase of Cosmopolitan species common in lower latitudes (*Profundimitra*, *Sconsia*, *Sveltia*, *Ficus*, *Conus*, and *Dalium*)

occurred along with the first extensive record of the Caribbean taxa in the region (*Amusium*, *Nodipecten*, *Clementia*, *Torcula* and *Muracyprea*) (del Río, 2021). Late Miocene molluscan faunas from northern Patagonia show the presence of Endemic and Cosmopolitan genera, while Paleoaustrian taxa virtually disappeared. Mollusca recorded a renewal of the tropical Caribbean taxa with the extinction of middle Miocene ones and the occurrence of *Leopecten*, *Chionopsis* and *Hexacorbula* (del Río, 1990, 2021).

Terrestrial earliest Miocene floras include forests of low diversity represented mostly by Gondwanan families while Neotropical elements became widely reduced. Early-mid Miocene floras, however, peak in diversity, with a consistent presence of Neotropical elements (Zamalao, 2000; Falaschi et al., 2012; Caviglia and Zamalao, 2014; Barreda and Palazzesi, 2021). The earliest expansion of coastal shrubs and herbs occurred such as *Cressa*, Ephedraceae, Amaranthaceae, Asteraceae and Calyceraceae (Barreda and Palazzesi, 2007; Barreda et al., 2008; Palazzesi et al., 2010). After a short re-greening, these arid-adapted taxa (except grasses) rose to dominance by the late Miocene.

Early Miocene mammal communities show open-habitat species coexisting with an increasing number of forest-dwelling elements with many arboreal clades, including the first records of primates in Patagonia. Browsing rather than grazing herbivores dominated the mammal faunas. Other forest indicators include low-crowned browsing litopterns, porcupines, and sloths. Interestingly, early-mid Miocene sloths include three paleo-autecological groups (Toledo et al., 2016): 1) arboreal and semi-arboreal folivores (*Euchloeops*, *Hapalops*, *Schismotherium* and *Analcimorphus*, but probably also *Pelecycodon*); 2) semi-arboreal mixed consumers of leaves, fruits and tubers with digging capabilities (e.g. mylodontids *Nematherium* and *Analcitherium*), and 3) terrestrial folivores capable of facultative climbing (e.g. *Prepothierium*). Many early Miocene mammal lineages persisted into the middle Miocene, but the number of arboreal mammal clades declined and euhippodont notoungulates and rodents became more common, suggesting progressively more open and xeric environments. Marine mammals also experienced drastic taxonomic and ecological changes; the cetacean fossil record from Patagonia documented both the diversification of some living cetacean clades, and the origin of key ecological strategies (Buono et al., 2017).

3.5. Pliocene

During the Pliocene, a shallow marine incursion is recorded along coastlines of central and southern Patagonia. This incursion accumulated sediments, interpreted as having been deposited in a coastal environment (e.g. Rovere et al., 2020). The timing of this flooding event is constrained to the 5.23–4.69 Ma (Zanclean, early Pliocene) based on Sr-isotope ages obtained from molluscan shells (del Río et al., 2013; Rovere et al., 2020). The early Pliocene assemblages include *Moir-echlamys*, *Kolmeris*, *Scalariocardita*, *Carditella*, and *Eucallista*, reported from the eastern coast of Santa Cruz Province (del Río et al., 2013). Except for a few mammalian taxa and remains coming from Río Negro Province in northernmost Patagonia (see Alberdi et al., 1997, and literature cited therein), floras and mammal faunas have not yet been recovered from Pliocene sediments in this region.

4. Discussion

The Chicxulub asteroid impact and Deccan volcanism of the Cretaceous–Paleogene boundary led to a major restructuring of Cenozoic biotas (e.g. Carvalho et al., 2021). In South America, the long-term response of ecosystems appears to have been pronounced in lower latitudes, although severe and brief interruptions have been detected –particularly in the floras– in the southernmost latitudes of the continent (Barreda et al., 2012; Stiles et al., 2020). After a minor warming event across the Cretaceous/Paleogene boundary (66.05 Ma), the Paleocene experienced cycles of warming and cooling episodes. The early

Paleocene warming trend mirrored a major global rise in sea level, which caused one of the most important Cenozoic flooding events in Patagonia (Fig. 3, EP). The abundant and diverse marine elements (i.e. dinocysts and molluscs) indicate a continuous connection between sub-Antarctic regions and northern tropical –Tethyan and Atlantic– regions. The cool marine incursions in southern Patagonia contrast with warmer conditions in northern Patagonia detected by dinocysts, indicating fluctuations of relatively low and high sea surface temperatures and/or the existence of some latitudinal temperature gradients in the South Atlantic by the earliest Paleocene. Terrestrial Paleocene faunas and floras from Patagonia indicate intercontinental dispersals from either lower American latitudes (e.g. metatherians, palms), the Weddellian province (e.g. monotremes, and gondwanatheres) or Australasia (e.g., casuarinas), while other groups might have evolved and diversified in the Patagonian region (e.g. legumes, daisies, xenungulates). The unusually high diversity of floras detected in the early Paleocene, including many angiosperms, mirrored the increasing diversity of dental morphologies in herbivorous mammals.

Earth's climate warmed from the late Paleocene to the early Eocene (59–54 Ma), although global sea-level appears not to have risen significantly (Miller et al., 2020). Floras document a strong increase in diversity by the early Eocene (Fig. 2), including many Australasian elements (e.g. *Eucalyptus*, *Gymnostoma*, *Akania*, and *Agathis*), supporting the strong southern biogeographic connection (Gandolfo and Zamalao, 2021; Reguero and Goin, 2021). Patagonian land faunas were diverse in the early Eocene, being largely represented by small insectivorous (e.g. Derorhynchidae, Sternbergiidae), omnivorous (e.g. Protodidelphidae) and browsing (e.g. Isotemnidae) mammals. A close biogeographic link to Western Antarctica is sustained by the presence of common floristic (e.g. Nothofagaceae, Proteaceae) and faunistic (e.g. derorhynchid and woodburnodontid metatherians and litoptern placentals) elements. By mid-Eocene times, southern Patagonia became flooded by a shallow marine incursion, with subtropical as well as endemic molluscs and dinocysts (Fig. 3, ME-EO). High frequencies of the warm-water dinocyst species *Enneadocysta dictyostila* along with the occurrence of tropical and subtropical molluscan assemblages (González Estebenet et al., 2016; del Río, 2021; Fernández et al., 2021) reflect the onset of the Middle Eocene Climatic Optimum (or MECO), at about 40 Ma. The record of dinocysts indicate the influence of Antarctic waters and the confluence of Pacific water flows, mirroring an early opening of the Sea of Hoces (Drake Passage) according to González Estebenet et al. (2014). Terrestrial floras in the southernmost regions of Patagonia show an increasing diversity during the MECO, about 40 % richer than pre-MECO and post-MECO (Fernández et al., 2021). Tropical elements –particularly palms– increased in abundance and diversity, supporting the idea that warm-adapted lineages penetrated into the highest austral latitudes during greenhouse periods (Fernández et al., in press, Fig. 2). Faunas include a strong representation of carnivorous metatherians, xenarthrans, and notoungulates, some of the latter characterized by an incipient trend towards hypsodonty (e.g. Archaeopithecidae). Hypsodonty is often viewed as a guide to an herbivorous diet that includes grasses and taken as a signal of grassland ecosystems, but a more likely selective agent for hypsodonty is the ingestion of abrasive soil or grit resulting from cropping plants close to the ground in generally open habitats, not necessarily grasslands (Kay et al., 1999; Madden, 2015).

By the late Eocene and early Oligocene, the onset of a long-lasting cooling episode (or coolhouse state) occurred linked with the first major glaciation of Antarctica (Westerhold et al., 2020). A sea level drop and an increasing aridity trend is supported by sedimentological (e.g. Bellosi, 2010) and paleontological (e.g. Dunn et al., 2015) evidence. Mesic floras with abundant canopy-forming trees and ferns appear to have been present in southern Patagonia, particularly beside rivers and along estuaries (Olivero et al., 1998; Fernández et al., 2021). However, palm-dominated woodlands existed further north, in central Patagonia (Zucol et al., 2010; Dunn et al., 2015), where palm-fueled fires are known to have promoted the spread of open ecosystems during the late

Eocene and early Oligocene, although briefly decreased at 33.58 Ma, coincident with the Antarctic glaciation (Selkin et al., 2015). Hence, the presence of large areas occupied by flammable biomes appear to have occurred in southern South America, contributing not only to the spread of open-habitat ecosystems but also to the development of a mixed-mosaic of habitats. Grasses, however, remained virtually absent based on pollen and phytolith records during the early Oligocene (Palazzesi and Barreda, 2012; Selkin et al., 2015; but see Bellosi et al., 2021). Faunas underwent the most dramatic metatherian turnover of the South American Cenozoic during these times, the “Bisagra Patagónica” (Patagonian Hinge) event (Fig. 2), according to Goin et al. (2010), probably in response to the marked changes in Patagonian landscapes. The feeding habit of mammals appears to have been more frugivorous, omnivorous, or insectivorous during the Paleocene-Eocene, and including more seeds, hard fruits, and/or abrasive food items) during the early Oligocene. Hence, the rodent-like adaptations among South American metatherians further support the idea of a more open, and drier landscape.

During the late Oligocene, a marine incursion occurred (Fig. 3, LO) and preserved the first plant indicators of relatively open coastal vegetation with elements common today in salt-marshes and open areas (e.g. Amaranthaceae, Ephedraceae, and Asteraceae); interestingly, these families briefly rose during subsequent aridification events of the Miocene and became dominant in the present-day Patagonian steppe. Some tropical taxa such as Areaceae (palms) and Fabaceae (legume family, subfamily Caesalpinioideae) probably formed patches of seasonally-dry forests (Barreda and Palazzesi, 2021). However, at least in coastal central Patagonia, Gondwanan canopy trees were still dominant (e.g. Araucariaceae, Podocarpaceae, and Nothofagaceae).

During the early-mid Miocene (Fig. 3, EM-MM), the sea invaded extensive areas of Patagonia, with a maximum flooding at 20–19 Ma (Fig. 3, EM). The presence of dinocyst assemblages containing out-ershelf species preserved in sediments along the present-day coastline supports the notion that this Miocene flooding event was widespread in Patagonia (Palamarczuk and Barreda, 1998). Molluscan faunas experienced a major reduction of Paleogene tropical taxa along with an influx of a subtropical southern assemblage (Neogene Southern elements). Floras show a major drop in diversity by the early Miocene (~22 Ma), probably following the global cool conditions and a local dry episode detected in Patagonia (Bellosi and González, 2010). This floristic deterioration mirrored an incipient rise of shrubs (e.g. *Ephedra*) and arid-tolerant gymnosperms (e.g. *Araucaria*). Mammalian faunas adapted to woodlands and to more open vegetation patches became diverse and abundant (e.g. ungulates). By the early-mid Miocene, there was a peak in floristic diversity, with an increasing presence of tropical elements, coincident with the record of the oldest Patagonian primates along with other forest-dwelling elements, including low-crowned browsing litopterns, porcupines and sloths (Fig. 2); open-habitat elements (e.g. notoungulates) were also common. The splendid diversity of floras and faunas in Patagonia during this time reflects the Miocene Climatic Optimum (Barreda and Palazzesi, 2021), a transient warming event that represents one of several major interruptions in the long-term cooling trend of the past 38 Ma (Coolhouse state *sensu* Westerhold et al., 2020). This warming peak is also recorded by the marine molluscan (del Río, 2021) and dinocyst (Guler et al., 2021) assemblages (Fig. 3) which reveal the presence of a new suite of tropical genera (Caribbean elements) that occurred in these southern latitudes. This zenith of Neogene diversity culminates with the virtual disappearance of key arboreal faunas (e.g. primates, and arboreal sloths) and tropical floras (e.g. palms) by ~14 Ma (Fig. 2), when earth's climate transitioned from a relatively warm to a cooler phase with reestablishment of permanent ice sheets on Antarctica. In this context, the Andean uplift may have even accentuated the effects of the cooling trend by promoting the increasing aridity that typically characterizes the region today; the onset of the rain-shadow effect appears to have developed from the mid-late Miocene in eastern Patagonian landscapes (Palazzesi et al., 2014). By this time in the

marine realm, dinocyst assemblages exhibit abrupt decrease in warm-water taxa and the extinction of the thermophilic species *Dapsilidinium pseudolligerum* and *Hystrichokolpoma rigaudiae*; molluscs also record the extinction of tropical taxa.

During the late Miocene (~10 Ma), a minor marine incursion occurred in northern Patagonia (Fig. 3, LM). The associated dinocysts and molluscan faunas suggest that the sea waters were warmer than present, as indicated by the presence of tropical and Caribbean elements, in agreement with the globally recognized Tortonian Thermal Maximum (Westerhold et al., 2020). The dominance of euhyposodont herbivorous taxa in the late Miocene is consistent with the further retraction of forest to the Andean region and the expansion of open habitats across eastern Patagonia. Among these open-habitat elements, grasses (family Poaceae) still occurred in very low frequencies during the late Miocene, at least in northern Patagonia. Recent debate on the timing of the early rise and expansion of such family on Patagonian hinterlands has been instructive. The more traditional view suggests that grasses expanded early in the Eocene in this region; this may have been the main force to the development of hyposodoty, as previously mentioned. However, palynologists have failed to find a terrestrial fossil plant assemblage dominated by grasses, except of course in Quaternary deposits (e.g. Mancini et al., 2008), when the present-day steppe was well developed. The analysis of fossil phytoliths recovered from terrestrial deposits opened up the door to a more realistic model in which grasses developed across Patagonian hinterlands, but as a secondary element, usually within palm-dominated ecosystems, until the mid-Miocene. Although these contrasting hypotheses are under current debate, we are confident that large extensions of open-habitats existed in central Patagonia, particularly during increasing arid periods. However, the current paleobotanical evidence (i.e. phytoliths and pollen grains) does not support the presence of grasslands until the Pliocene (Palazzesi and Barreda, 2012; Dunn et al., 2015; although see Bellosi et al., 2021 for a different interpretation). The current grass-dominated Patagonian steppe probably evolved during the ice age world of the Plio-Pleistocene.

Overall, we find a rather close coupling between (and within) our multiple proxy-records throughout the Cenozoic, with peaks of thermophilic species during greenhouse (hothouse and warmhouse) conditions, decreasing during coolhouse conditions, and falling still further when Antarctica became fully glaciated and the Andean-range uplifted. Although our overview highlights the potential of multidisciplinary collaborations, it by no means represents a conclusive synthesis of the evolution of Cenozoic biotas and environments (and eventually paleoecosystems) from Patagonia but, rather, a brief updated review, mainly based on the fossil record.

In this special issue, entitled 'Reconstruction of Cenozoic ecosystems from Patagonia on the basis of multiple independent proxy records', we selected papers that address only a small subset of the vast number of paleontological disciplines. We hope it will encourage and inspire more needed research activities in the near future; our field urgently needs multidisciplinary (and probably interdisciplinary, Nicolescu, 2014; Baker, 2017) collaborations either to unify concepts or to tackle a broad range of scientific questions. Several significant challenges remain in the years ahead, including an improved understanding of paleogeographic changes that undergone in this part of the globe just prior to and during the Cenozoic, with further evidence from other sources (e.g. sedimentology, geochemistry, ichnology, taphonomy, among others). Also, there is a crucial need to quantify patterns of biodiversity from terrestrial and marine fossil records using either adjusted for sample-size methods or more robust estimates in order to better understand how independent proxy-records responded to past climate change. Addressing these and other challenges will undoubtedly improve our understanding of biotic evolution and environmental dynamics across the Cenozoic at these high southern latitudes.

Authorship statement

Conception and design of study: Luis Palazzesi, Sergio F. Vizcaíno, Viviana D. Barreda; analysis and interpretation of data: Luis Palazzesi, Sergio F. Vizcaino, Viviana D. Barreda, José I. Cuitiño, Claudia J. del Río, Francisco Goin, M. Sol González Estebenet, M. Verónica Guler, María Alejandra Gandolfo, Richard Kay, Ana Parras, Marcelo A. Reguero, María del Carmen Zamalao.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

The invitation of Andrés Folguera to guest-edit the present Special Issue "Reconstruction of Cenozoic ecosystems from Patagonia on the basis of multiple independent proxy records" is much appreciated by LP, SFV and VDB. Two anonymous reviewers improved an earlier version of this manuscript. Most of the plant and animal silhouettes of our Fig. 2 comes from vecteezy.com. Funding was provided by grants from Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) and Agencia Nacional de Promoción Científica y Tecnológica (ANPCyT). MAG thanks support from National Science Foundation grants DEB-1556136 and EAR-1925552.

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