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# Macroevolutionary changes in the fossil plant record: Key examples from the Cretaceous-Paleogene of Patagonia, Argentina

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ABSTRACT

Clearly, past and present plant diversity is due to the many evolutionary processes that are the manifestation of the organisms' responses to changes in the environment. Most current evolutionary studies (such as population genetics, epigenetic mechanisms, phylogeography, and phylogenetics) provide information on a few generation-times and are focused on microevolutionary events. Some of these studies have as major goals the estimation of divergence times, construction of phylogenies, and explanations of biogeographical distributions. Nevertheless, the majority of these studies use fossils only as calibration points and mostly ignore critical information that only fossils can provide about the course of evolution in general. Herein, we reevaluate macroevolutionary changes that are critical for understanding past and present diversity and provide concrete examples in deep time (Cretaceous-Paleogene) from several sites in Patagonia, Argentina. We discuss Extinction, Retraction, Expansion, Diversification, and Coevolution (Codiversification) processes that have significantly shaped modern Patagonian vegetation.

## 1. Introduction

The equator, the imaginary line of 0° (zero degrees) latitude that divides modern Earth into two equal hemispheres, was originally "discovered" during the "Geodesic Expedition of 1736–1744" (Taylor, 1999). Equator derives from the Latin word *aequator* which means "make equal"; however, the hemispheres as defined by this imaginary line are quite different in geography, proportion of land and water, topography, and climate. The Northern Hemisphere (NH) comprises 70% of all land while the Southern Hemisphere (SH) contains the remainder (30%) of land; and the proportion water-land is 70%–30% for the NH whereas for the SH is 94%–6%. Remarkably, between latitudes 30° and 60° north, the ratio of water to land is about 1:1 but between 30° and 60° south it is approximately 16:1 (Fig. 1). The temperatures in the NH are cooler than those of the SH, and in winter the variation of temperature in the SH is less than for the NH. The continentality of the NH and oceanicity of the SH have considerable effects on the climate and therefore results in completely different scenarios for plant distributions. The complex relationships among these geographical differences and global environmental factors (e.g. oceanic currents, winds, etc.), in addition to other more local disturbances (such as floods, fires, volcanic eruptions, etc.) and the role of vegetation dynamics in initiating changes, have had and continue having significant effects in the life history of ecosystems over short and long term periods of time (Bonan, 2008). Interestingly, the equatorial areas of both hemispheres show high plant diversity (Barthlott et al., 1996) while clearly that diversity

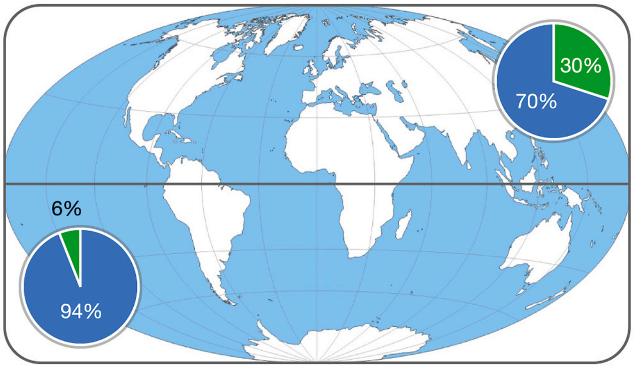

**Fig. 1.** Northern and Southern Hemispheres ratio water (blue):land (green).

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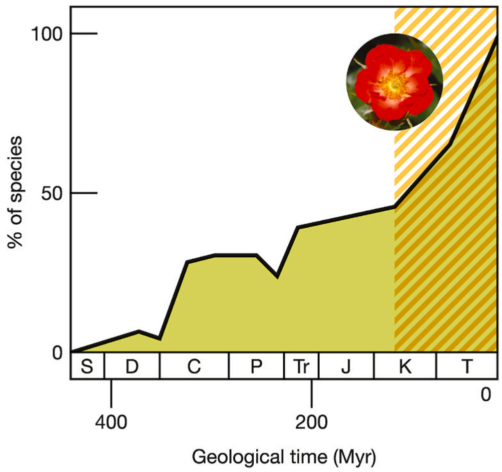

**Fig. 2.** Changes in vascular land plant diversity through geological time showing the sharp raise in angiosperm diversity after the Cretaceous. (Modified from Niklas et al., 1983, based on approximately 18,000 fossil plant species citations).

decreases towards the poles where at the extreme on the Antarctic Peninsula the angiosperms are only represented by two species (the caryophyll *Colobanthus quitensis* and the grass *Deschampsia antarctica*). Equatorial peaks in species richness are typical of marine and terrestrial ecosystems and have characterized the planet since the Devonian (Signor, 1990).

However, plant diversity peaks increased dramatically at the end of the Cretaceous and during the early Cenozoic with the rapid radiation and diversification of the flowering plants (see for example Knoll, 1984, 2003; Niklas et al., 1983; Niklas, 1997; Crepet et al., 2004; Friis et al., 2011, Fig. 2). During this time period, the angiosperms became the dominant group of plants in the ecosystems and it is during the Neogene that numerous geologic events (such as marked worldwide continental uplift, separation of major continental landmasses, the establishment of the Circumpolar Antarctic Current, and the continental collision between the Indian and Eurasian plates) occurred that effectively partitioned the tropics, contributing to the origination of the high diversity hot spots that persist today (Signor, 1990; Niklas, 1997; Crame, 2001).

Considering the Americas, that span in both hemispheres (Fig. 3), the United States of America (NH) comprises approximately 10 million km$^2$, contains 7% of global angiosperm diversity, and ca. 1.4% are endemics (Flora of North America, 1993+). Tropical Brazil has portions in both hemispheres and covers approximately 8.5 million km$^2$ of continuous land area and has 20% of global angiosperm diversity of which 56% are endemics. However, endemism may be much higher because almost 43% of the area of the Amazon Basin has never been sampled (Souza-Baena et al., 2014; Brazilian Flora Group, 2015). Argentina, completely in the SH, with a tropical to polar climate, is about one third of the area of Brazil (~2.7 million km$^2$), and comprises only 3% of global angiosperm diversity, and has approximately 0.5% of endemics (Zuloaga and Morrone, 1996).

Argentina (continental Argentina + Argentine Antarctica), situated between 23° 22' and 90° S, includes land areas from the tropics to polar zones, and is the perfect "area" for understanding latitudinal gradient distribution and for explaining modern austral vegetation in general. Of particular interest within Argentina is Patagonia, the southernmost portion of South America. Patagonia comprises the last 1600 km of continental South America and includes part of Chile and Argentina, and is characterized by many different biomes. If the Andes are used to divide Patagonia into west and east, its eastern portion consists primarily of flat, dry plains called the "Patagonian steppe" or shrub-grassland in the northern part a warm desert vegetation type known as the Monte (combination of dry scrub and limited grassland, similar to the Sonoran Desert of North America). The Andes and the area west of them (mostly Chile) are densely covered by numerous glaciers that plunge into a complex system of lakes and in the southernmost part narrow fjords, and its flora comprises several vegetational types among them the *Araucaria* forests and woodlands, the Valdivian and Subantarctic Forests, *Austrocedrus*/*Maytenus* woodlands, the Andean *Nothofagus* dominated forests, and the (high altitude) alpine vegetation (Cabrera and Willink, 1973; Gut, 2008). These vegetational types and highly diverse flora are the result of many microevolutionary (short time) and macroevolutionary (deep time) changes.

Clearly, past and present plant diversity is due to the many evolutionary processes that are, mainly, the manifestation of the organisms' responses to changes in the environment. Most current evolutionary studies (such as population genetics, epigenetic mechanisms, phylogeography, and phylogenetics) are focused on microevolutionary events which provide information only for time-spans of a few generations. Nonetheless, for understanding and explaining general patterns of diversity, one needs to look in the context of deep time. Macroevolutionary processes reveal patterns of relationships among extinct forms that are obviously interwoven with those patterns among living taxa (Novacek and Wheeler, 1992). This implies addressing the fossil record from the point of view of recognizing specific patterns in deep time as fossils provide critical information when arriving to conclusions about evolution in general. Understanding macroevolutionary processes can provide unique insight for comprehending the diversity of life forms (evolutionary differences of major taxonomic groups, Levinton, 2001), explain how and why this diversity came to be and allow full understanding of any kind of interaction between a species and its environment (Wing et al., 1992). Fundamentally, as stated by Bromham and Cardillo (2019; page 1) "macroevolution focuses on changing patterns of biological diversity across time, space and lineages".

It is generally agreed (e.g. Simpson, 1953; Stebbins, 1974; Futuyma, 1997) that speciation processes are the fundamental starting points in the entire course of macroevolution as a speciation event occurs when a genetically homogenous species/population splits into two or more species/populations that undergo genetic differentiation followed by reproductive isolation; therefore, speciation is tied to the origination of clades, including those that diversify and succeed and become what we call "major clades". This is the essence of macroevolution. Unfortunately, these two primary processes (speciation and diversification) are

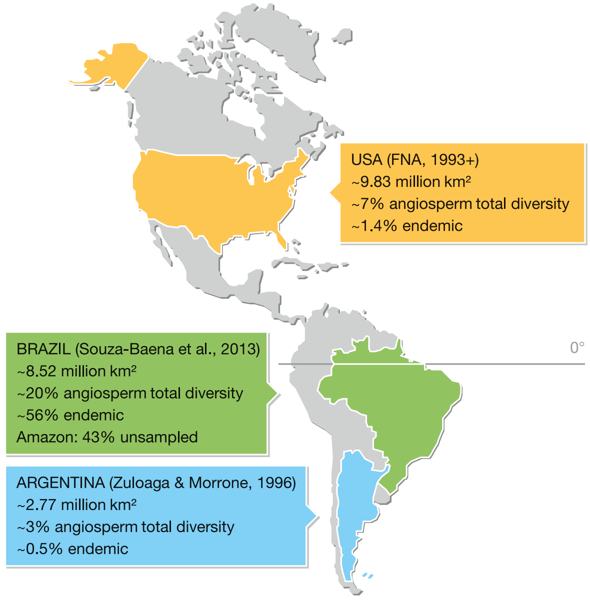

**Fig. 3.** Map of The Americas showing the comparative differences in angiosperm diversity and endemism between both hemispheres.

impossible to observe directly in the fossil record. Yet, the fossil record provides the first appearances of taxa and that is the only concrete evidence of their initial existences. Even though the fossil record is incomplete and only a small fraction is known, it implies multiple speciation, origination and diversification events that occurred since the beginning of life on Earth (see Benton, 1995; Knoll, 1984; 2003; Porter, 2004; Javaux, 2007).

Based on speciation and origination events in conjunction with geological, environmental, and climatic factors, one can actually decipher other macroevolutionary changes in the life of a taxon/community in deep time. Herein, we reevaluate some macroevolutionary events that are critical for understanding past and present plant diversity in Patagonia, Argentina and provide concrete examples in deep time (Cretaceous-Paleogene= CP). Patagonia was affected by several geological and paleoclimatic changes during the CP and the co-occurrent effects of these changes caused drastic modifications in the paleoenvironments that, in turn, had ecological and evolutionary consequences that were manifested in high taxonomic levels (clade, families) and had significantly shaped modern Patagonian vegetation. Here we merely discuss and provide examples of important biological events of Extinction, Retraction, Expansion, Diversification, and Coevolution (Codiversification).

## 2. Macroevolutionary events

### 2.1. Extinction

Based on the fossil record, two types of extinctions are recognized: extinction and extirpation (Behrensmeyer et al., 1992). Extinction is commonly defined as the loss of all the individuals of a taxon which implies a “global” or worldwide extinction (e.g. ammonites and dinosaurs). But, one can also observe the loss of all individuals and populations of a taxon at a particular geographic area, this event is called “extirpation” and basically is a local extinction event. There are many examples of extinctions of plant lineages in the fossil record (e.g. early vascular plants such as the rhyniophytes, the seed ferns, and the Glossopteridales, Taylor et al., 2009), but the majority occurred before the Cretaceous.

### 2.1.1. Global extinction or Extinction

**Cheirolepidiaceae.-** An example of plant “global” extinction observed in Patagonia includes the large conifer family Cheirolepidiaceae. This extinct conifer clade was distributed worldwide and had a long history, starting in the Triassic and becoming extinct near the end of the Mesozoic. It comprises several types of plants, characterized for producing only *Classopollis* pollen (Taylor et al., 2009). The family is represented in Patagonia by several genera based on leaves and male and female cones including the genera *Brachyphyllum* (e.g. Carrizo et al., 2019), *Pararaucaria* (Escapa et al., 2012, 2013, 2017), *Tomaxellia* (Archangelsky, 1968; Villar de Seoane, 1998), and *Kachaikestrobus* (Del Fueyo et al., 2008) and by *Classopollis* pollen that have been recorded in many Patagonian formations (Villar de Seoane, 2014; Villar de Seoane and Archangelsky, 2014). Remarkably, *Classopollis*, although mostly extinct by the end of the Cretaceous in most places around the world (Zavialova et al., 2010), reappeared in the latest Maastrichtian in Patagonia and had a peak profile after the K/Pg boundary in the region where it was an important component of its Danian floras. The last record of *Classopollis* dates from the Paleocene (see Barreda et al., 2012 and citations therein) of Patagonia. Thus, based on available fossil evidence, the last known species in this clade were found in Patagonia, prior to global extinction.

### 2.1.2. Local extinction or Extirpation

In Patagonia, extirpations or local extinction events during the Cretaceous/Paleogene are more common and better documented than global extinctions. Extirpations are recognized in ferns, gymnosperms, and angiosperms, and are reflected at various taxonomic levels. Among the pteridophytes, the aquatic ferns *Paleoazolla* from the Maastrichtian La Colonia Formation and several species of *Azolla* also from the La Colonia Fm. and the Danian Salamanca Formation disappeared after the Paleocene (De Benedetti et al., 2018, 2020; Hermsen et al., 2019). Exceptional examples of extirpation come from the early Eocene Laguna del Hunco site in Chubut Province (LH), one of the most diverse Eocene floras known worldwide (Wilf et al., 2005). The LH flora includes taxa that today can be found extant in South America, Australasia, and Southeast Asia. The last fossil record of the South American ginkgophytes (Villar de Seoane et al., 2015 and citations therein) and the loss of the genera *Papuacedrus* (Cupressaceae, Wilf et al., 2009) and *Dacrycarpus* and *Dacrycarpites* pollen (Podocarpaceae, Wilf, 2012; Barreda et al., 2020) from South America were recorded at LH. Most outstanding is the disappearance of flowering plants at different taxonomic levels such as Akaniaceae at the family level (Romero and Hickey, 1976; Gandolfo et al., 1988), Schizomerieae (Cunoniaceae) at the tribe level (Jud et al., 2018; Jud and Gandolfo, 2021), and *Ceratopetalum* (Gandolfo and Hermsen, 2017) and *Castanopsis* (Wilf et al., 2019) at the generic level.

***Todea***.- The pteridophyte family Osmundaceae first appeared in Permian deposits worldwide, and in South America and the Antarctic Peninsula is well documented in Mesozoic sediments. However, its Cenozoic record in Patagonia was unknown until recently. Carvahlo et al. (2013) described sterile and fertile fronds collected at LH that were placed phylogenetically as belonging to the leptopteroid genus *Todea*, one of the four extant Osmundaceae genera. Additionally, Bomfleur and Escapa (2019) reinforced the presence of the genus based on the finding of a silicified trunk. Modern *Todea* no longer occurs in South America, and comprises two species found in southern Africa, Australia and New Zealand and one species endemic to New Guinea. Today, living leptopteroid ferns are widely distributed in the Southern Hemisphere although they are not found in South America (Kramer, 1990; Parris, 2001); however in the late Paleozoic and the Mesozoic the clade was found in both hemispheres and in southern South America they were abundant during the Triassic and Jurassic. The finding of *Todea* in the LH flora suggests that the lineage survived at least until early Eocene (Carvahlo et al., 2013) and therefore it was extirpated sometime after that.

***Agathis***.- The family Araucariaceae is mostly restricted today to the SH and has three living genera, *Araucaria*, *Agathis*, and *Wollemia*, but only *Araucaria* survives today in South America (Dettmann and Clifford, 2005). The family has an abundant Mesozoic and Cenozoic macrofossil record in Patagonia, mainly represented by *Araucaria* wood, leaves, and reproductive structures (Panti et al., 2012 and citations therein). Recently, Wilf et al. (2014) reported the first fossils of *Agathis* in Patagonia consisting of vegetative and reproductive remains. Escapa et al. (2018) reported leaves related to *Agathis* from the uppermost Maastrichtian Lefipán Formation, and multiple reproductive and vegetative organs from the early Danian Salamanca Formation which, so far, constitute the oldest records of *Agathis* in Patagonia. *Dilwynites* pollen (fossil pollen genus with affinity to pollen of extant genera *Agathis* and *Wollemia*) was reported at the Early Cretaceous to the early Eocene sediments in Patagonia (Villar de Seoane and Archangelsky, 2014; Macphail et al., 2013; Escapa et al., 2018; Barreda et al., 2020). Notably, Escapa et al. (2018) found *Dilwynites* in situ within pollen sacs of *Agathis*.

Other fascinating examples of extirpation from Patagonia are the family Casuarinaceae and the genus *Eucalyptus*. Modern *Eucalyptus* and Casuarinaceae strictly occupy the Malesian-Australian-Melanesian region but in the past they have a widespread gondwanic distribution.

**Casuarinaceae.-** Modern Casuarinaceae comprises four genera, however, only the genus *Gymnostoma* is known to be present in the fossil record of Patagonia. Frenguelli (1943) described the first fossil remains of Casuarinaceae from the LH flora as *Casuarina patagonica*; additional fossils, including numerous branchlets, infructescences, and male inflorescences with *Haloragacidites* pollen grains in situ, collected in the same sediments were studied by Zamaloa et al. (2006). These authors concluded that the fossils actually belong to the segregate genus *Gymnostoma*. Fossil pollen related to Casuarinaceae, currently assigned to the fossil species *Haloragacidites harrisii*, was also reported in southern and central Patagonia from the late Maastrichtian Lefipán Fm. (Barreda et al., 2012) to the Oligocene Rio Leona Fm. (Barreda et al., 2009), with abundant records during the Eocene (Zamaloa et al., 2006). Thus far, there are no records for the family in Patagonia after the Oligocene.

***Eucalyptus***.- The oldest record worldwide of the classical Australian genus *Eucalyptus* (Myrtaceae) comes from Patagonia where it is only known from specimens collected at the LH site. The suite of fossils, comprising leaves, infructescences, isolated capsules, flower buds, and flowers has been undoubtedly placed within the *Eucalyptus* crown group (Gandolfo et al., 2011; Hermsen et al., 2012). The most noteworthy specimen is one exquisitely preserved flower with *Myrtaceidites eucalyptoides* pollen preserved in situ in the anthers (Zamaloa et al., 2020). Interestingly, there are no other macrofossils or pollen recorded in South America for the genus.

### 2.2. Retraction

Retraction is defined as the sudden or progressive reduction of the geographic area occupied by a taxon or population (Futuyma, 1997; Behrensmeyer et al., 1992; Bromham and Cardillo, 2019). It can be explained as the result of two different processes which are in response to changes in the environment and that lead either to reduction in the area occupied by the taxon/taxa (Geographic Retraction) or to its partial extinction/extirpation (Diversity Retraction). Here, in the context of Patagonia, we treat “Geographic Retraction” as the reduction or displacement of a taxon or population to lower latitudes which results in smaller area(s) of distribution whereas “Diversity Retraction” is the result of a decrease in diversity at the generic or species level, and as a consequence, there is an evident loss of the occupied area by that taxon/population. In both cases, the locations in which a taxon or taxa have persisted while becoming extinct elsewhere can ultimately become “refugia.” These two processes are contrary to “Expansion” and “Diversification” events (treated below).

There are many examples in Patagonia of retraction for ferns (e.g. Dicksoniaceae, Gandolfo et al., 2014), gymnosperms (e.g. *Austrozamia*, Wilf et al., 2016), and angiosperms (e.g. Anacardiaceae- *Striatricolporites gamerroi* and Ulmaceae-*Ulmoideipites patagonicus*, Barreda et al., 2020; Araceae, Gallego et al., 2014; Solanaceae-*Physalis*, Wilf et al., 2017; Deanna et al., 2020 ) during the Cretaceous-Paleogene.

#### 2.2.1. Geographic and Diversity retraction

**Arecaceae**.- One of the best case studies for both “Geographic” and “Diversity” retractions, is the family Arecaceae (true palms), because it clearly demonstrates that, in general, macroevolutionary events are not isolated or independent but mostly occur concurrently. Today, the palm family is widespread in tropical and subtropical areas, inhabiting many different environments (Dransfield et al., 2008). However, during the Cretaceous to the Paleogene, palms were distributed in both hemispheres reaching very high latitudes (Eldrett et al., 2009; Pross et al., 2012; Reichgelt et al., 2018). In South America, modern Arecaceae only grows naturally north of 35°S latitude while its fossil record spans the Lower Cretaceous of Patagonia to the Pliocene of Argentine Mesopotamia in the north of the country (Futey et al., 2012 and citations therein). Patagonian fossils assigned to palms include stems and pollen and are found at outcrops of Lower Cretaceous age, reaching early Miocene sediments in high latitudes. The oldest records based on stems are specimens assigned to the morphogenus *Palmoxylon* (Ancibor, 1995; Ottone, 2007; Martinez, 2012); other *Palmoxylon* remains were recovered from the Paleocene sediments (Romero, 1968; Petriella, 1972; Arguijo, 1979, 1981). Aside from these, no other records are known of this morphotype in Patagonia, although it reappeared in the Pliocene of the Entre Rios Province (~35°S; Lutz 1980, 1984). Futey et al. (2012) described *Tripylocarpa aestuaria,* the only known Argentinean fossil palm fruits, which belong to the Subtribe Attalainae, Tribe Cocoseae, Subfamily Arecoideae. These were collected at the Salamanca Formation (Danian) at Estancia Las Violetas Locality, Patagonia. Zucol et al. (2007) and Strömberg et al. (2013) also reported the presence of palm phytoliths at the Middle Eocene-Early Miocene Sarmiento Formation, at Gran Barranca. Nevertheless, the family is best represented in the Patagonian fossil record by its pollen (e.g. *Confertisulcites*, *Liliacidites*, *Longapertites*, *Monosulcites*, *Sabalpollenites*, and *Spinizonocolpites* just to name a few of them) even extending its presence into the Maastrichtian of Seymour Island near the Antarctica Peninsula (e.g. *Gemmamonocolpites pilulus*, *Arecipites,* and *Monosulcites minutiscabratus*; Baldoni and Barreda, 1986; Askin, 1994). The oldest palm pollen grains come from the Lower Cretaceous (Barremian-Aptian) of the Austral Basin (Martinez et al., 2016); they are *Spinizonocolpites* tetrads and monads that show close affinities to the extant genus *Nypa*. In the Maastrichtian-Danian Lefipán Formation, Barreda et al. (2012) recovered two species of *Arecipites*, *Longapertites*, and *Spinizonocolpites*. But it is during the Paleocene when the highest diversity of palm pollen is registered (e.g. *Monosulcites pseudospinosus*, *Proxapertites operculatus*, *Arecipites minutiscabratus*, *Longapertites patagonicus*, *L. andreisii*, *Spinizonocolpites*, and *Monogemmites gemmatus*; Palazzesi and Barreda, 2007; Volkheimer et al., 2007) at the Austral and Golfo de San Jorge Basins. Noteworthy is the fact that the record of palm pollen declined rapidly after the Paleocene, and so far, there are no Arecaceae palynological records for the Eocene and only a few records of *Arecipites* and *Spinizonocolpites* are documented at the Oligocene Santa Cruz Formation (Austral Basin; Barreda, 1997, Nañez et al., 2009). The last record for palms is *Arecipites subverrucatus* from the early Miocene Chenque and Monte León formations (Barreda, 1997; Barreda and Palamarczuk, 2000). The record from Monte León is considered to be the southernmost and last record of palms in Patagonia. Plainly, Arecacaeae suffered both Geographic and Diversity retractions as indicated by its fossil record.

#### 2.2.2. Geographic retraction

**Marsileaceae**.- The aquatic fern genus *Regnellidum* is currently restricted to a very small area in northeastern Argentina, southern Brazil, and Uruguay (De la Sota and Mitchel, 1970; Tryon and Tryon, 1982; Kramer, 1990), although during the Cretaceous megaspores and microspores with affinities to *Regnellidum* were widespread in both hemispheres (see Cúneo et al., 2013 and citations therein). Cúneo et al. (2013) described *Regnellidum thomas-taylorii* based on a group of roots, rhizomes, leaves, isolated leaflets, and sporocarps resembling features of the modern genus. These structures were found in intimate association with *Molaspora lobata* megaspores and *Crybelosporites* cf. *pannuceus* microspores which are considered to belong to the genera *Regnellidum* and/or *Pilularia* (another marsileaceous genus). These megafossils were only recovered from deposits of the late Cretaceous La Colonia Formation that outcrops in north-central Chubut Province. There is definitely a substantial reduction in the area occupied by the genus.

**Juglandaceae**.- The genus *Alatonucula*, a juglandoid fossil genus, based on fruits collected at the Laguna del Hunco site (Hermsen and Gandolfo, 2016) represents the only confirmed macrofossil Juglandaceae in Patagonia. Its placement within the family Juglandaceae subfamily Engelhardioideae was confirmed by phylogenetic analyses. Barreda et al. (2020) also reported the presence of *Plicatopollis* pollen

(Jungladaceae) at the same site, remarkably representing almost 24% of all the palynoflora at the site. These fossil genera are of particular interest because they exemplify a compelling Laurasian biogeographic signal, as the current distribution of the family is predominantly in the Northern Hemisphere (Stone, 1993), with the exception of a few engelhardioids which extend south across the Equator into the neotropics, and for *Juglans*, with a single species that grows naturally in the Andes of northern Argentina (Stone et al., 2009). The family is also represented in Patagonia by *Plicatopollis* pollen dating from Paleocene sediments (Zamaloa and Andreis, 1995; Volkheimer et al., 2007; Melendi et al., 2003; Barreda and Palazzesi, 2007; Quattrocchio et al., 2012), while there are no post-Eocene pollen records in the region.

### *2.2.3. Diversity retraction*

**Salviniaceae**.- The case of the heterosporous water fern *Azolla* is one of the most representative events of Diversity retraction in Patagonia. Today, *Azolla* is the only extant aquatic fern found in Patagonia, although *Salvinia* and the three genera of Marsileaceae (*Marsilea*, *Pilularia*, and *Regnellidium*) are distributed north of Buenos Aires province in subtropical to tropical areas (Tryon and Tryon, 1982). Nevertheless, the Patagonian fossil record of heterosporous aquatic ferns started in the Lower Cretaceous and extended to the Paleocene (De Benedetti et al., 2019). Although the record is mostly based on megaspores and microspores, macrofossils assigned to Marsileaceae and Salviniaceae have been recently reported from the Maastrichtian La Colonia and the Danian Salamanca formations, Chubut (Cúneo et al., 2013, 2014; Hermsen et al., 2014, 2019). The genus *Arcellites* constitutes the first appearance of aquatic ferns in Patagonia. Originally described from Aptian-Albian sediments of the Austral Basin outcropping at the Santa Cruz province, it comprises three species (Baldoni and Taylor, 1988; Villar de Seoane and Archangelsky, 2008). By the Cenomanian, another species of *Arcellites* appeared together with the first record of the genus *Ariadneasporites,* also from the Austral Basin (Santamarina et al., 2018). It is during the Campanian-Maastrichtian that they reached their highest diversity (from two genera to seven recognized genera) in Patagonia with records from 15 formations all over Patagonia. This diversity drastically declined during the Paleocene as their presence is only registered in four formations (De Benedetti et al., 2019).

## *2.3. Diversification and Expansion*

Expansion is defined as the progressive extension of the area occupied by a taxon or population whereas diversification implies the evolutionary increase of the number of genera/species in a clade and is usually accompanied by divergence in phenotypic characters (divergence is basically the evolution in increasing differences between lineages in one or more characters). Expansion sometimes occurs in tandem with diversification events. Notably, both diversification and expansion depend on speciation and origination processes (Futuyma, 1997; Bromham and Cardillo, 2019).

Obviously, expansions and diversifications during the Cretaceous/Paleogene are most evident among the angiosperms as they raised, diversified, and became the dominants in terrestrial ecosystems (Crane, 1987; Crepet et al., 2004; Friis et al., 2011). There are numerous examples of expansion and diversification events recorded in Patagonia (such as Proteaceae, Gonzalez et al., 2007; Rhamnaceae, Jud et al., 2017). Nonetheless, the most remarkable example is the iconic Southern Hemisphere genus *Nothofagus* (Nothofagaceae).

*Nothofagus* is restricted to the SH with representatives in Australasia (Australia, New Zealand, Papua New Guinea, and New Caledonia) and southwestern Patagonia where they are the main component of the southern South American temperate forests. Extinct taxa are found in Antarctica, Australia, New Zealand, and Patagonia (e.g. Romero, 1986; Dettman et al., 1990; Hill, 2001) as well, confirming that previously the family was widely distributed and quite diverse in geologic time. Several fossil species based on remains of leaves have been described as belonging to *Nothofagus* (e.g. Caviglia and Zamaloa, 2014; Dusén, 1899; Hünicken, 1955, 1967, 1971; Panti, 2019; Romero, 1986; Vento et al., 2016) and numerous species placed within the fossil wood *Nothofagoxylon* (Ancibor, 1990; Brea, 1993; Pujana, 2008, 2009) are frequently reported for Patagonian Cretaceous and Tertiary sediments. However, the most notable fossils are the pollen grains. *Nothofagus* pollen, known in the fossil record as *Nothofagidites*, is stratigraphically and geographically the most useful of all the Nothofagaceae fossils as it is often very well preserved, morphologically distinctive, and abundantly produced (Hill, 2001). Extant *Nothofagus* includes four monophyletic subgenera (e.g. Hill and Read, 1991; Hill and Jordan, 1993; Manos, 1997; Setoguchi et al., 1997). *Nothofagus* subgenera are *N.* subgenus *Brassospora* (New Caledonia and New Guinea), *N.* subgenus *Fuscospora* (New Zealand and South America), *N.* subgenus *Lophozonia* (Australia, New Zealand, and South America) and *N.* subgenus *Nothofagus* (southern South America) and each is characterized for producing very distinctive pollen grains.

To date, the oldest known occurrences of *Nothofagidites,* recovered from late Campanian sediments of the Antarctic Peninsula, are considered to be those of the "ancestral type" (= no placement within any extant subgenera). This evidence confirms a high latitude southern origin for the family during the early Campanian in the region encompassing Australasia-Antarctica-southern South America (Dettmann et al., 1990). Interestingly, the pollen types corresponding to the four modern subgenera appeared simultaneously in the Maastrichtian of southern Patagonia (Dettmann et al., 1990; Romero and Zamaloa, 1997). Between the Maastrichtian and the early Eocene, *Nothofagidites* is uninterruptedly found in low proportions in Patagonian palynofloras, and it is during the middle Eocene that it became the dominant component within the associations in the south and central Patagonia (e.g. Rio Turbio and Osorno formations, Markgraf et al., 1996). Towards the end of the middle Eocene until the early Miocene, there is an increase in diversity recorded by the presence of at least 13 species of *Nothofagidites.* As a consequence, there is an expansion of its geographical distribution in Patagonia reaching its northernmost record and a peak of diversity with 13 formally described species (Dettmann et al., 1990; Romero and Zamaloa, 1997). In addition, there are *Nothofagidites* records that so far are not assigned to any previously described species, indicating the possibility that they can be representatives of new fossil species. Hill (2001) suggested *Nothofagus* reached its highest diversity globally during the late Oligocene-early Miocene which is probably when the Patagonian *Nothofagus* diversity peaked as well. Altogether, this demonstrates that *Nothofagus* acquired its high diversity during the Paleogene and early Neogene expanding the area where they lived.

At present, there are three subgenera and nine species of *Nothofagus* in South America, distributed from 33°S to Tierra del Fuego (56° S) at both sides of the Andes, and all of the species are endemic to South America/Patagonia. *Nothofagus* subgenus *Nothofagus* (*N. antarctica*, *N. betuloides*, *N. dombeyi*, *N. nitida*, and *N. pumilio*) is restricted to South America and it is widely distributed between 33° and 56°S whereas *N.* subgenus *Lophozonia* (*N. alpina, N. obliqua*, and *N. glauca*) and *N.* subgenus *Fuscospora* (*N. alessandri*) have a relictual distribution between 33° and 41°S in northern Patagonia (including Chile; Amigo and Rodriguez-Guilián, 2011).

Nevertheless in the Patagonian fossil record, the four modern subgenera of *Nothofagus* and the "ancestral type" are recognized in the Maastrichtian (for example subgenus *Brassospora* is represented by *N. dorotensis* and *N. fuegiensis*, subgenus *Fuscospora* by *N. saraensis*, subgenus *Nothofagus* by *N. rocaensis*, and subgenus *Lophozonia* by *N. americanus*, and *N. kaitangataensis* that belongs to an ancestral type; Romero and Zamaloa, 1997) until the early Miocene, covering all of western Patagonia, from Neuquén province to Tierra del Fuego (e.g. Zamaloa, 2000). A continuous record between the early Miocene and the Holocene is unknown, and several studies of Quaternary sediments reveal that subgenera *Lophozonia* and *Fuscospora* were already absent at low latitudes (43°- 56°S; e.g. Heusser et al., 1992, 2000) confirming the significative retraction of both subgenera from the south towards the north due to climatic changes during the pre-Quaternary and the Quaternary that vastly affected their habitat (Donoso, 1996). Comparing its past and current distribution, there is an obvious geographic retraction of both subgenera after the Miocene. During the Maastrichtian, *N.* subgenus *Brassospora* comprised at least four *Nothofagidites* species that were broadly distributed in Patagonia, however it distinctly declined towards the end of the Paleogene. The last and southernmost record dates from the early Miocene Cullen Formation, Tierra del Fuego (Zamaloa, 2000) and the northernmost from the Navidad Formation, Chile (34° S; Barreda et al., 2011). After that *Nothofagus* subgenus *Brassospora* became extirpated from South America.

### *2.4. Coevolution (Codiversification)*

Although coevolution has several meanings (Thompson, 1989; Futuyma and Agrawal, 2009), a commonly accepted definition is the mutual evolution of two (or more) ecologically interacting species, each of which evolves in response to selection imposed by the other. Among the recognized cases of coevolution in the plant fossil record is the evolution of insect pollination in angiosperms during the Cretaceous-Paleogene (for example Crepet, 1984; Hu et al., 2008; Labandeira et al., 1994) and the coevolution of angiosperms and frugivores since the early Eocene (e.g. Tiffney, 1984; Herrera, 2002; Eriksson, 2016). However, to our knowledge, there are no confirmed reports of host (plant)-parasite (plant) coevolution events in the fossil record. There are numerous examples in various families of modern parasitic plants (such as members of the Santalales; Nickrent et al., 2010) for which the host is another flowering plant. Specialist parasites tend to infect narrow groups of closely related host species (that is, species within the same genus; genus within the same family). At the same time parasite speciation can occur in response to host speciation and, in consequence, co-speciation is more frequent when host specificity is high (Norton and Carpenter, 1998). The Patagonian fossil record of *Nothofagus* and *Misodendrum*, the sole genus of the aerial hemiparasitic family Misodendraceae (mistletoe) provides us with concrete evidence of plant-plant codiversification in deep time.

*Misodendrum* comprises eight species endemic to the austral South American *Nothofagus*-dominated temperate forests. They are all host specific naturally parasitizing species of *Nothofagus* and very rarely other flowering plants or conifers (e.g. Skottsberg, 1913; Rossow, 1982; Zavaro et al., 1997; Kuijt and Hansen, 2015; Amico et al., 2019). The fossil record of Misodendraceae consists exclusively of dispersed pollen grains allocated to the form genera *Sparsipollis, Compositoipollenites*, or to *Misodendrum*; and the oldest record of the family comes from subsurface sediments of southern Patagonia dated as Eocene in age (about 45 Ma, Zamaloa and Fernández, 2016). Although scarce, the fossil pollen record indicates that the family was present in southern Patagonia by the Eocene and persisted to the present (with sporadic records in the Oligocene and Miocene). During the Quaternary, *Misodendrum* pollen records are quite abundant and widespread in western and southern Patagonia indicating that by the Quaternary the genus had already reached its current geographic distribution (Zamaloa and Fernández, 2016). Evidently, *Misodendrum* was present during the Eocene, at the same time that *Nothofagus* was already diversifying and becoming dominant in the temperate forests (see above). Coincidently, based on molecular data, Vidal-Russell and Nickrent (2008) proposed that aerial parasitism occurred first in Misodendraceae ca. 80 mya. (early Campanian) which is when the first appearance of *Nothofagidites* is recorded (Dettmann et al., 1990). Vidal-Russell and Nickrent (op. cit.) also highlighted the possibility that both taxa, *Nothofagus* and *Misodendrum*, codiversified during the Cretaceous. The fact that fossils of Misodendraceae are so far only known from Patagonian deposits points to a local origin and diversification of the group linked to the diversification of the South American *Nothofagus* that resulted in the endemism of the family Misodendraceae.

Okubamichael et al. (2016) pointed to multiple factors such as host availability, abundance and compatibility, seed dispersal vectors, as well as history and environmental conditions that affect the interaction of parasites and their hosts and determine host specificity. Norton and Carpenter (1998) were the first to emphasize the relevance of both space and time (linked to the host abundance) in the coevolutionary processes undergone by host and parasite as they clearly stated that “The relative host abundance is the key to host specificity. As relative host abundance is variable, host specificity must be seen as dynamic, variable in both space and time, and dependent on the opportunities available in any one time or place” (Norton and Carpenter, 1998, page 102).

Several authors noticed that, although the geographic range of the host plant *Nothofagus* extends to other Gondwanan landmasses, *Misodendrum* is restricted to southern South America, in contrast to other *Nothofagus* parasites such as the fungus genus *Cyttaria* (e.g. Zavaro et al., 1997; Vidal-Russell and Nickrent, 2007; Kuijt and Hansen, 2015). Nevertheless, published data suggest that *Misodendrum* species mainly parasitize species of *Nothofagus* subgenus *Nothofagus* (the most abundant and widest distributed of the South American subgenera of *Nothofagus*) (Orfila, 1978; Rossow, 1982; Zavaro et al., 1997; Flora Argentina online, 2020; Amico et al., 2019), indicating if not a strict specificity at least a local host specificity or a marked preference of the mistletoe for *N.* subgenus *Nothofagus*, so members of *N.* subgenus *Nothofagus* would be its primary host. Thus, since the primary host, *N.* subgenus *Nothofagus,* is currently endemic to South America this would explain the restricted presence of the parasite, *Misodendrum*, in South America as well.

Based on this evidence, we hypothesize that the preferred host *Nothofagus* subgenus *Nothofagus*-parasite *Misodendrum* association was established before the Eocene; although due to the coincidental timing of the appearance of *Nothofagus* and *Misodendrum* in the fossil record during the Campanian, it is possible that they have coevolved and codiversified much earlier and that by the Eocene the association was already well-established. Nonetheless, additional evidence is necessary to corroborate this hypothesis. Independently, this intimate, long-term and dynamic (*sensu* Norton and Carpenter, 1998) association may have changed over time when other *Nothofagus* subgenera co-dominated the Patagonian forests, and it could have been maintained by the stability of preferred host availability through time and space (Norton and Lange, 1999), reflected today in the endemism of both partners of the association.

## 3. Final remarks

There is no doubt that for any evolutionary biologist one of the most intriguing facts is that probably 99% of the Earth biota comprises extinct taxa and therefore life in deep time is almost a complete mystery. This intensely indicates that knowledge of life evolution on Earth is extremally biased towards current living organisms. Nevertheless, even when imperfect and incomplete, the fossil record is the only window to past life. It is because of the fossil record that we are certain that life on Earth started at least 3.5 Ga (Schopf, 2000; Westall, 2004), that plant diversity has been increasing for the last 700 my, and increasing very rapidly since about 120 my when the flowering plants appeared for first time in the record (Fig. 2; Taylor et al., 2009). We also know, once more based on the fossil record, that evolutionary processes have occurred since the beginning of life on Earth and it is due to those processes, combined with many abiotic factors, that the structure, composition, and function of terrestrial ecosystems changed throughout time.

Patagonia, the southernmost portion of the Americas, has a rich plant fossil record that provides concrete examples of evolutionary processes (Box 1) in deep time. Here we introduce only a few ones which clearly demonstrate the crucial role of Patagonia for studying the dynamics of macroevolutionary processes.

Evidently, some of the examples presented are the result of the combination of more than one evolutionary process; for example *Nothofagus* (coevolution, diversification, expansion, and retraction) and

**Box 1**

Definitions of macroevolutionary processes as presented in text.

**Global Extinction:** Loss of all individuals and populations of a taxon.

**Local Extinction (Extirpation):** Loss of all individuals and populations from a particular geographic area.

**Retraction (general):** Sudden or progressive reduction of the geographic distribution of a taxon or population.

**Geographic Retraction:** Reduction or displacement of a taxon or population to lower latitudes which results in smaller area(s) of distribution.

**Diversity Retraction:** Decrease in diversity at generic or species level, and as a consequence, there is an evident loss of the occupied area by that taxon/population.

**Expansion:** Progressive extension of the area occupied by a taxon or population.

**Diversification:** Evolutionary increase of the number of species in a clade, usually accompanied by divergence in phenotypic characters.

**Coevolution (Codiversification):** Strictly, the joint evolution of two (or more) ecologically interacting species, each of which evolves in response to selection imposed by the other.

Arecaceae (geographic and diversity retractions), while others are manifestations of a single event such as *Eucalyptus* (local extinction or extirpation) and Cheirolepidaceae (global extinction following its extinction in the NH).

Of particular interest is the *Nothofagus-Misodendrum* association because, at least to our knowledge, this represents the first “fossil” record of coevolution (codiversification) between two plant taxa; and this new evidence strongly supports the presence of this association during the Campanian-Maastrichtian and also suggests an Eocene codiversification.

Nonetheless, these examples demonstrate that paleontological (paleobotanical) studies are fundamental for the discovery and understanding of biological patterns in the history of lineages over long periods of time (Wing et al., 1992). For example, Huyse et al. (2005) suggested that host-parasite coevolution should be addressed at both macro and microevolutionary levels and they emphasized that macroevolution processes provide the critical background for understanding the origins of host-parasite relationships. This statement can be and should be easily applied for all macroevolutionary processes.

All clades (families/genera/species) were (are) affected by past events; consequently, any study focused on evolution should be approached in an integrative manner and should include data from the fossil record when available. In summary, ignoring such critical information is detrimental to understanding the history of life on Earth.

## 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.

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