



An Oligocene microthermal forest dominated by *Nothofagus* in Sierra Baguales, Chilean Patagonia: Response to global cooling and tectonic events



Néstor M. Gutiérrez^{a,f,*}, Juan Pablo Pino^b, Jacobus P. Le Roux^{a,c}, Viviana Pedroza^{a,c},
José Luis Oyarzun^d, Luis Felipe Hinojosa^{b,e}

^a Departamento de Geología, FCFM, Universidad de Chile, Plaza Ercilla 803, Santiago, Chile

^b Departamento de Ciencias Ecológicas, Universidad de Chile, Ñuñoa, Santiago, Chile

^c Centro de Excelencia en Geotermia de los Andes, Plaza Ercilla 803, Santiago, Chile

^d Parque Geológico y Paleontológico La Cumbre-Baguales, Km 385 Norte Ruta N° 9, Magallanes, Chile

^e Instituto de Ecología y Biodiversidad (IEB), Santiago, Chile

^f Centro de Investigación, Desarrollo e Innovación de Estructuras y Materiales IDIEM, Universidad de Chile, Chile

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ABSTRACT

A large fossil leaf assemblage (> 3700 specimens) is reported from the Oligocene Río Leona Formation in the Sierra Baguales of Chilean Patagonia. The association comprises 29 species but is dominated by *Nothofagus* genera, which constitutes 65% of specimens. The collection can be classified as a Mixed Palaeoflora of the Austral-Antarctic association. Stratigraphic analysis of the assemblage indicates a decrease in species diversity and richness over time, which was accompanied by species turnover. Quantitative studies of foliar morphology (CLAMP, Leaf Margin Analysis) indicates cool-to-cold and dry climatic conditions, with a Mean Annual Temperature of 9.2 °C, a relatively high seasonality in temperature and precipitation, and a Mean Annual Precipitation of 931 mm. *Nothofagus* only became dominant in southeastern Patagonia during the Rupelian, coinciding with a marked global cooling period linked to the initiation of glaciation in Antarctica about 34 Ma. The decrease in precipitation following this event is attributed to the development of a rain shadow to the east of the rising Southern Patagonian Andes, which must have been of the order of 1000 m or more for topographic climate forcing to take effect. This contrasts with the rain shadow development east of the Andes at lower latitudes, which was mainly manifested after the middle Miocene.

1. Introduction

In South America, there are very few studies showing the behavior of vegetation during cooling episodes (Hinojosa, 2005). Floras of Oligocene age in South America are scarce and records only exist in Patagonia, in the late Eocene to early Oligocene Río Guillermo Formation near Santa Cruz (Panti, 2011) and in the Lago Argentino sector in the late Oligocene Río Leona Formation (Césari et al., 2015). For both floras, cold-temperate, humid climates are assumed (Panti, 2011; Césari et al., 2015). In the Sierra Baguales (SB) of the Última Esperanza Province, we collected fossil leaves from the Río Leona Formation, which is of Rupelian age (Gutiérrez et al., 2017). These were used to investigate the response of vegetation, in terms of diversity and composition, to tectonic and climatic changes such as the opening of the Drake Passage to the east and south, uplift of the Southern Patagonian Andes to the west, and global climatic variations during the Oligocene.

The distribution and floral composition of the present southern South American forests resulted from a long history of interaction between the biota, geological processes and climate changes during the Cenozoic (Romero, 1978; Romero, 1986; Arroyo et al., 1996; Hinojosa and Villagrán, 1997; Villagrán and Hinojosa, 1997; Troncoso and Romero, 1998; Hinojosa, 2003, 2005; Wilf et al., 2005; Quattrocchio et al., 2013). Paleoclimate estimates of the Mean Annual Temperature (MAT) based on the relationship between plant leaf physiognomy and climate (Wolfe, 1979, 1995; Wilf, 1997; Wing, 1998; Jacobs, 1999; Gregory-Wodzicki, 2000; Burnham et al., 2001; Hinojosa, 2005; Hinojosa et al., 2011; Peppe et al., 2011) showed that during the Paleogene, MAT values were 0.6–12 °C warmer than the present MAT in southern South America (Wilf et al., 2005; Hinojosa, 2005; Iglesias et al., 2007; Quattrocchio et al., 2013; Hinojosa et al., 2016; Gutiérrez et al., 2017). During the Eocene Climatic Optimum, the MAT was 9–12 °C higher than at present, but then declined considerably until the

* Corresponding author at: Departamento de Geología, FCFM, Universidad de Chile, Plaza Ercilla 803, Santiago, Chile.

E-mail address: gutierrezn@ug.uchile.cl (N.M. Gutiérrez).

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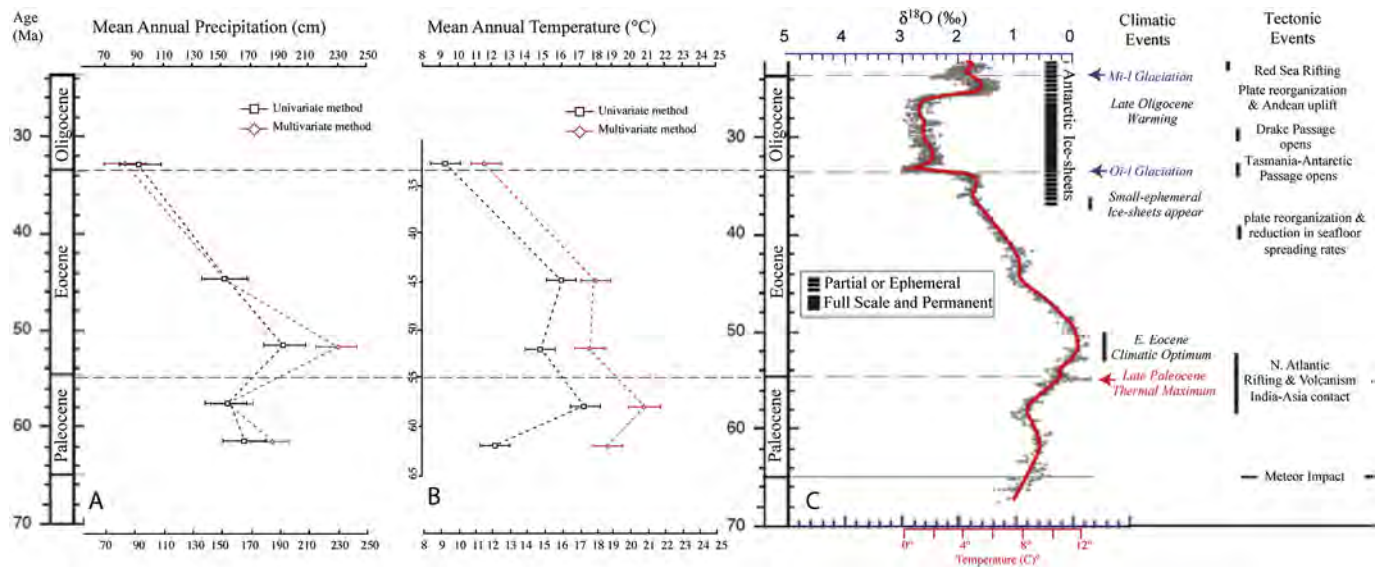


Fig. 1. Synthesis of climatic and tectonic events of Patagonia during the Cenozoic. A) Mean Annual Precipitation using univariate and multivariate method in fossil leaves (Gutiérrez et al., 2017; Hinojosa, 2005); B) mean Annual Temperature using univariate and multivariate method in fossil leaves (Hinojosa, 2005); C) global oxygen isotope curve (Zachos et al., 2001).

Oligocene, reaching minimum values that were only 0.6–1 °C warmer than present MAT (Hinojosa et al., 2011; Peppe et al., 2011; Quattrocchio et al., 2013). This decline in temperature coincides roughly with the Bartonian Rupelian Cooling (41–28 Ma) of Le Roux (2012) (Fig. 1).

Palynological analysis of the tropical zones has shown that changes in plant diversity and composition during the Cenozoic were sensitive to global temperature changes (Jaramillo et al., 2006). For example, fossil palynomorphs show that the very rapid climate warming experienced around 56 Ma during the Thanetian Ypresian Warming or Paleocene-Eocene Thermal Maximum, triggered an increase in plant diversity, which accompanied high amounts of rainfall and elevated temperatures (Rull, 1999; Jaramillo, 2002; Jaramillo et al., 2006). Between the Paleocene and middle Eocene (65.5–40.4 Ma) the palaeoflora of southern South America registered a change in its floral composition, passing from Tropical Gondwana Palaeoflora to Subtropical Gondwana Palaeoflora. The fossil floras of Laguna del Hunco and Río Pichileufú (Argentinian Patagonia; ~42°–45°S), for example, show high diversity indices at around 52 Ma during the Eocene (Wilf et al., 2005; Iglesias et al., 2007) in what may constitute evidence of the climate change proposed by Rull (1999) and Jaramillo (2002) for this moment in geological time. After the end of the Eocene (35.9 Ma), however, the Subtropical Gondwana Palaeoflora (characterized by warm elements, with modern distributions predominantly in the modern Neotropics and Australasian areas) was replaced by a Mixed Palaeoflora characterized by the increase of the current Austral-Antarctic distribution element, and equivalent proportions of the Neotropical and Pantropical warm elements (Hinojosa and Villagrán, 1997, 2005; Hinojosa et al., 2006; Quattrocchio et al., 2013). The South American Mixed Palaeoflora first appeared in Antarctica during the Paleocene (Dusén, 1916) and expanded towards the north to reach 30°S during the Eocene. In the Oligocene, the Mixed Palaeoflora remained restricted to subtropical latitudes between 38° and 30°S (Romero, 1978; Romero, 1986; Hinojosa and Villagrán, 1997; Villagrán and Hinojosa, 1997; Troncoso and Romero, 1998; Hinojosa, 2003, 2005; Quattrocchio et al., 2013).

In this paper, we analyze the paleobotany and paleoclimate of the Rio Leona Formation, Oligocene of Chilean Patagonia based on a large fossil plant assemblage to assess changes following the Eocene-Oligocene boundary.

2. Materials and methods

2.1. Collection and preparation of fossils

A total of 3746 fossil leaves were collected (3000 at Barranca de las Hojas, BDH, and 746 at Alto Río Bandurrias, ARB), which are stored at the Geology Department of the University of Chile. Each fossil imprint was prepared using a Dremel pneumatic tool, and a code was assigned showing its locality and number. In both locations the surface area sampled did not exceed > 5 m², and a thickness of 0.5 m. The quality of preservation in the ARB locality is better than the fossils collected in the BDH. ARB presents a higher density of fossil leaves; in a rock sample with an approximate volume of 0.01 m³ it is possible to find between 10 and 30 fossils. In the BDH locality, the density is lower; in the same volume it was only possible to collect between 2 and 5 fossils.

2.2. Identification and classification

The morphological characterization and description of fossils were carried out using the terminology in the Leaf Architecture Manual (LAWG, 1999; Ellis et al., 2009). Diagnostic morphological characteristics were thus highlighted to define each morphotype and distinguish it from other similar morphotypes. The identification and assignment of the possible taxonomic affinities of the species were based on the comparison between morphotypes of the Bagueles fossil flora (BFF) and those of other fossil floras previously described for the Oligocene and Eocene in South America (Romero, 1978; Gandolfo, 1994; Panti, 2010; Panti, 2011; Césari et al., 2015). In addition, for the Nothofagaceae family we used the literature on fossil and extant *Nothofagus* taxonomy erected by Hill and Read (1991), although Heenan and Smissen (2013) recently suggested that morphological and molecular differences between the four subgenera are sufficient for these to be recognized as separate genera. However, we do not adopt this revision in the present study, in order to avoid confusion between modern taxonomy and the fossil record (Hill et al., 2015; Hinojosa et al., 2016). Finally, morphological similarities to family level were established between the Bagueles Fossil Flora morphospecies and living species of modern-day Chilean forests.

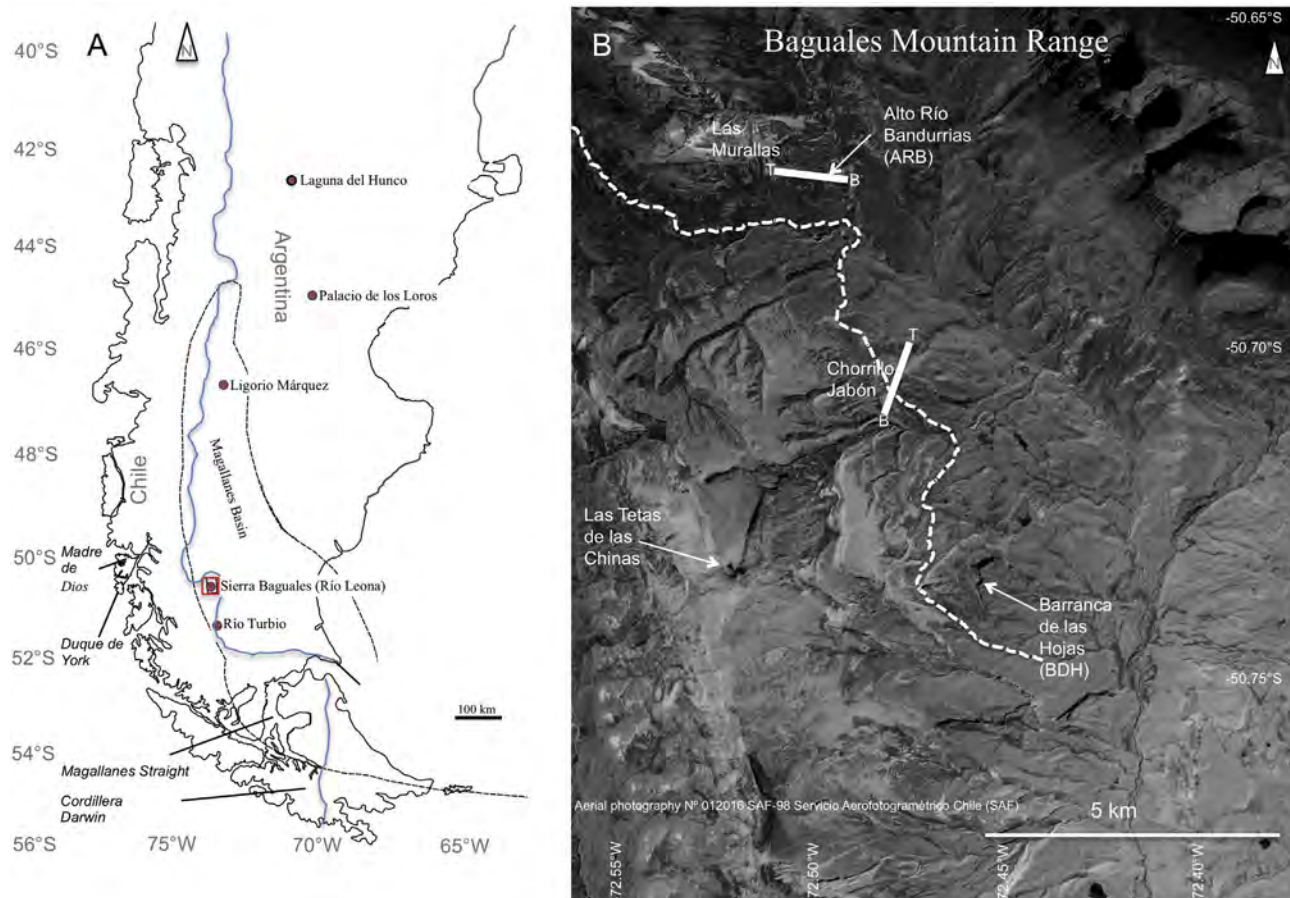


Fig. 2. Locality map of South America and the Sierra Baguales. A) Red dots show Tertiary fossil leaf localities in Patagonia: Laguna del Hunco, Palacio de los Loros, Ligorio Márquez, Río Leona, and Río Turbio. B) Show Baguales Mountain Range with Río Leona localities, Barranca de la Hojas (BDH) and Alto Río Bandurrias (ARB). White dotted line represents the contact between the Man Aike Formation and the Río Leona Formation. White line is the location of the stratigraphic columns. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.3. Paleoclimate univariate analysis

Univariate methods were used to estimate palaeoclimatic variations based on single foliar morphologies. Leaf Margin Analysis (LMA), which considers the positive relationship between the percentage of woody eudicot species with entire margins and the mean temperatures at present-day sites (Bailey and Sinnott, 1915, 1916), was employed to calculate Mean Annual Temperature. However, variations in this relationship have been detected that depend on the geographic region, as for example in Africa (Jacobs and Deino, 1996), Asia (Wolfe, 1979), Australia (Greenwood and Christophel, 2004), North America (Wolfe, 1993), Europe (Traiser et al., 2005), and South America (Gregory-Wodzicki, 2000; Kowalski, 2002; Hinojosa et al., 2011). In the estimation of Mean Annual Temperature for the fossil leaves of the BFF, regression analysis of the climatic and morphological variables of 161 sites in the CLAMP 3bSA database (Hinojosa, 2005) was carried out, employing the equations proposed for the South American model (Hinojosa et al., 2011) as well as the global model of Mean Annual Temperature (Peppe et al., 2011). Leaf Area Analysis (LAA) was used to estimate the Mean Annual Precipitation, which is based on the positive relationship between the mean of the natural log of foliar surface areas and the natural log of Mean Annual Precipitation (Hinojosa, 2005; Wilf et al., 1998).

2.4. Paleoclimatic multivariate analysis: CLAMP

The Climate Leaf Analysis Multivariate Program (CLAMP; Wolfe, 1990, 1993) establishes the relationship between 31 morphological

foliar characteristics of modern-day woody dicotyledonous species and the climatic variables associated with each site. The climatic variables include a dataset with 8 climatic variables, namely Mean Annual Temperature (MAT), Warm Month Mean Temperature (WMMT), Cold Month Mean Temperature (CMMT), Length of the Growing Season, which is the number of months with temperatures exceeding 10 °C (GROWSEAS) (Wolfe, 1993), Precipitation during the Growing Season (GSP), Mean Monthly Precipitation during the Growing Season (MMGSP), Precipitation during the Three Wettest Months (3WET), and Precipitation during the Three Driest Months (3DRY). The CLAMP analysis uses Canonical Correspondence Analysis as its statistical base (Ter-Braak, 1986), which is a direct ordering method placing the site in a multivariate space based on the morphological characteristics of the species that characterized the site and its climatic conditions.

2.5. Rarefaction analysis

The rarefaction method (Gotelli and Colwell, 2001) is used to compare the number of species when the samples differ in size. The species richness is estimated as a function of the size of the smallest sample (Gotelli and Entsminger, 2001). In the SB the species richness was estimated using rarefaction curves. The morphospecies diversity between the two sites was compared; additionally, a diversity analysis reaching “cutoff” was carried out, in this case using values of 200, 300, and 746 sample counts.

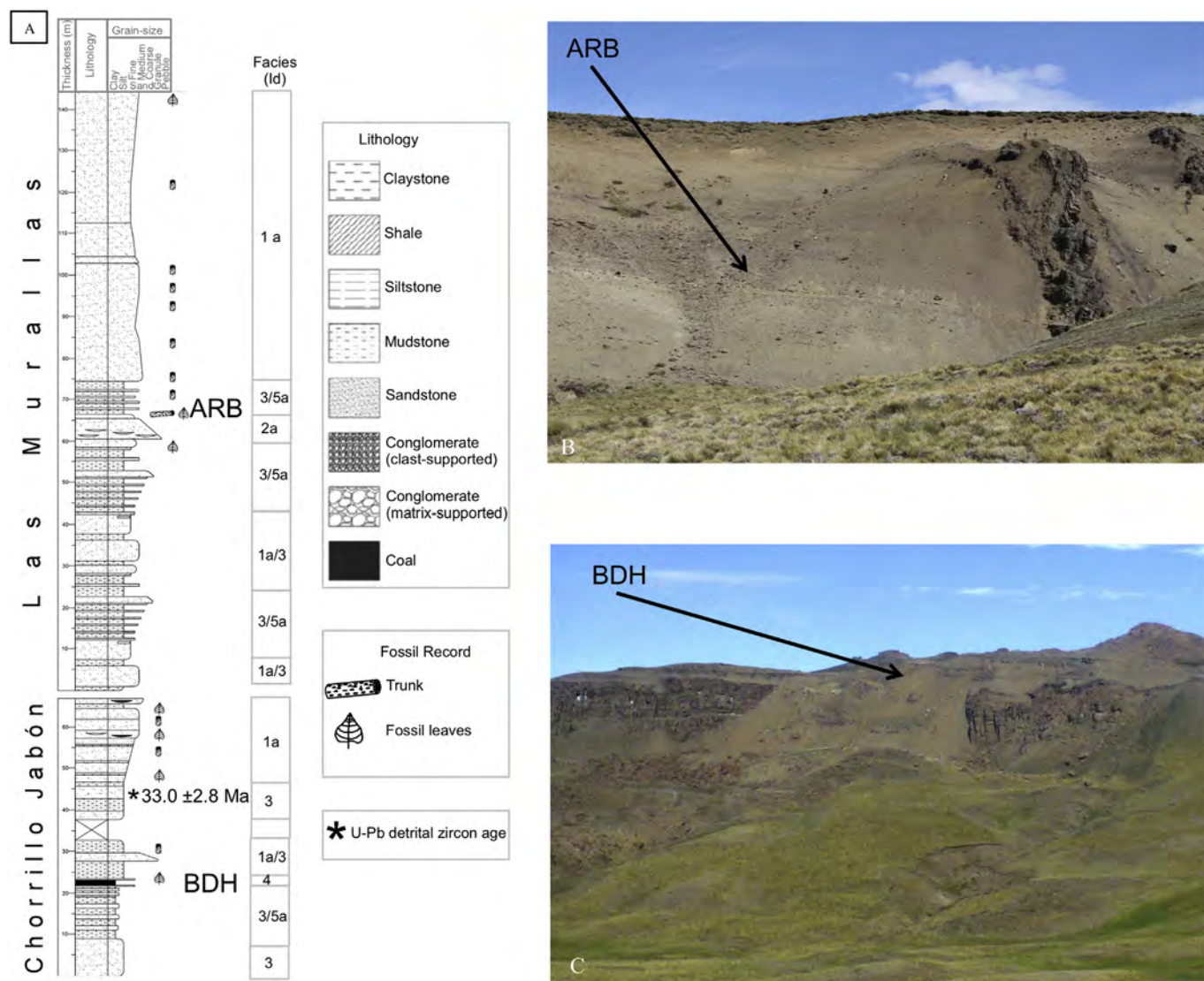


Fig. 3. Measured stratigraphic columns of Río Leona Formation at Las Murallas and Chorrillo Chico. A) Stratigraphic position of Alto Río Bandurrias (ARB) and Barranca de las Hojas (BDH) sites and U-Pb detrital zircon age (Gutiérrez et al., 2017). The facies code are explained in the Table 2; B) outcrops of Río Leona Formation at Las Murallas; C) outcrops of Río Leona Formation at Barranca de las Hojas.

2.6. Diversity analysis

At localities BDH and ARB the Shannon and Simpson diversity indices were estimated, as well as three species richness indices, namely CHAO2, Jackknife 1 and Jackknife 2.

The Shannon Index, abbreviated as “H”, also known as the Shannon-Wiener or Shannon-Weaver index, expresses the uniformity of the most important values as a function of all the sample species, measuring the mean uncertainty factor in predicting to which species an individual leaf belongs that is chosen randomly from a collection (Peet, 1974; Magurran, 1988; Baev and Penev, 1995). It thus assumes that the individual leaves are selected by chance and that all the species are represented in the sample, having a value of zero when there is only one species.

The Simpson Index of diversity, abbreviated as “λ”, shows the probability that two individuals chosen randomly from a sample are the same species. This is strongly influenced by the importance of the dominant species (Peet, 1974; Magurran, 1988). As its value is inverse to equality, the diversity can be calculated as 1 - λ (Lande, 1996).

CHAO 2 is an estimator of richness based on the abundance or incidence of species, taking account their presence/absence, in which the

number of expected species is estimated considering the relationship between the number of unique species (occurring in one sample) and the number of duplicate species (appearing in two samples).

The Jackknife estimation technique was introduced by Quenouille (1949, 1956). One of its most important applications is the reduction of bias, which can be summarized in two groups, namely bias reduction in punctual estimation, and the construction of confidence limits. The first-order Jackknife estimation (Jackknife 1) is based on the number of species present in only one sample, whereas second-order Jackknife (Jackknife 2) is similar to Jackknife 1, but also considers the number of species in two samples (Magurran, 2004).

3. Geological setting

The analyzed fossil floras are from Río Leona Formation assigned to the early Oligocene age (Rupelian) 33.0 ± 2.8 Ma based on U-Pb detrital zircon ages (Gutiérrez et al., 2017), which crops out in the Sierra Baguales northeast of the Torres del Paine National Park. This area forms part of the Magallanes or Austral Basin, as it is known in Chile and Argentina, respectively. The sediments of the Magallanes-Austral Basin accumulated between the Jurassic and Pliocene, forming

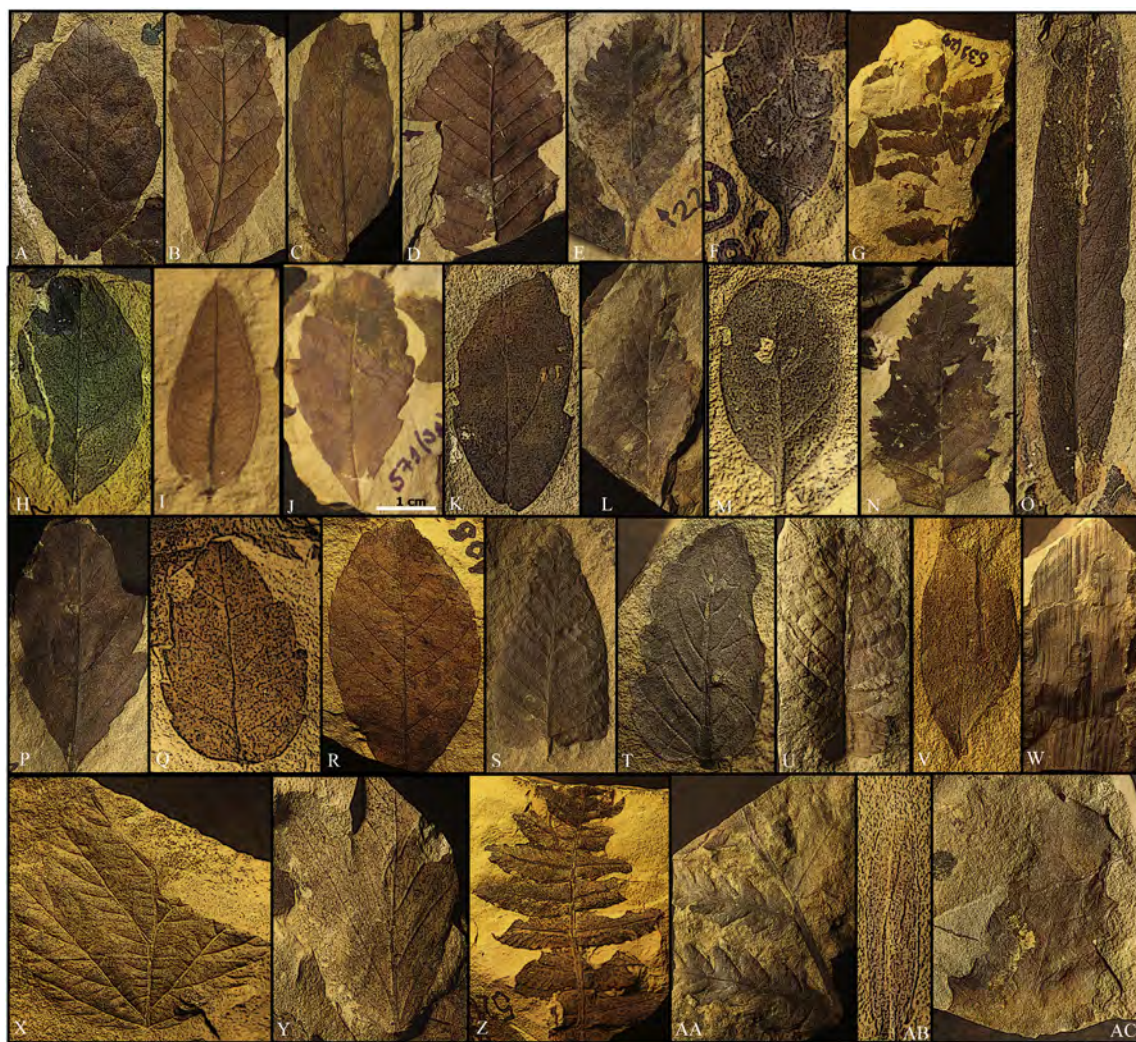


Fig. 4. Identified morphospecies in Baguales Fossil Flora. The samples will be stored in the paleobotany collection (PB) of the Museo Nacional de Historia Natural (MNHN) in Santiago (SGO) Chile, with the MNHN-SGO-PB code plus the number. A) MNHN-SGO-PB-1771; B) MNHN-SGO-PB-1770 Cunoneaceae?; C) MNHN-SGO-PB-1767; D) MNHN-SGO-PB-1769 *Nothofagus*; E) MNHN-SGO-PB-1768; F) MNHN-SGO-PB-1765; G) MNHN-SGO-PB-1755 Dryopteridaceae; H) MNHN-SGO-PB-1745 Monimiaceae; I) MNHN-SGO-PB-1764 Myrtaceae; J) MNHN-SGO-PB-1762 Sapindaceae; K) MNHN-SGO-PB-1761; L) MNHN-SGO-PB-1760; M) MNHN-SGO-PB-1757 Fabaceae; N) MNHN-SGO-PB-1763 *Nothofagus*; O) MNHN-SGO-PB-1759; P) MNHN-SGO-PB-1758 Fagaceae?; Q) MNHN-SGO-PB-1756 Gesneriaceae; R) MNHN-SGO-PB-1751; S) MNHN-SGO-PB-1749; T) MNHN-SGO-PB-1748; U) MNHN-SGO-PB-1746; V) MNHN-SGO-PB-1744 Lauraceae; W) MNHN-SGO-PB-1753 Poaceae; X) MNHN-SGO-PB-1750 Grossulariaceae; Y) MNHN-SGO-PB-1743 Grossulariaceae Z) MNHN-SGO-PB-1740 Blechnaceae; AA) MNHN-SGO-PB-1741 Dennstaedtiaceae; AB) MNHN-SGO-PB-1742 Podocarpaceae; AC) MNHN-SGO-PB-1747 Berberidaceae. 24 dicots) A; B; C; D; E; F; H; I; J; K; L; M; N; O; P; Q; R; S; T; U; V; X; Y; AC. 1 monocot) W. 3 pteridophytes) G; Z; AA. 1 conifer) AB.

a thick, slightly folded succession. In the Sierra Baguales, the succession comprises, from base to top, as follows: the Tres Pasos Formation (Campanian-Maastrichtian), the Dorotea Formation (Maastrichtian), the Man Aike Formation (early Eocene), the Río Leona Formation (early Oligocene), the Estancia 25 de Mayo Formation (early Miocene), and the Santa Cruz Formation (middle Miocene). The succession is capped by Pliocene lavas with an andesitic composition. At the Chorrillo Jabón (Base: 50°42'28.64"S, 72°28'37.01"W; top: 50°42'17.48"S, 72°28'11.86"W) and Alto Río Bandurrias sites in the SB (Base: 50°40'34.83"S, 72°29'27.06"W; top: 50°40'34.72"S, 72°29'56.82"W), a 210 m composite stratigraphic section was measured in the Río Leona Formation (Figs. 2, 3). The deposits formed on a coastal plain with meandering and braided river systems. The fossil record includes tree trunks, some in upright (life) position, and well-preserved leaves that accumulated in swamps and on overbank flood plains with reducing conditions. Within the Río Leona Formation, the stratigraphically oldest collection site is at BDH, where the leaves were collected close to its contact with the underlying Man Aike Formation. The ARB locality

represents the middle part of the Río Leona Formation.

4. Results

4.1. Diversity and richness estimation

The paleofloral diversity in the BFF totals 29 morphospecies (Fig. 3). Out of the total of 29 identified morphospecies, there are 24 morphospecies of dicot, 3 pteridophytes, 1 monocot, and 1 conifer (Fig. 4). Only 18 of the 29 morphospecies could be assigned to family level (Table 1). In the BFF, *Nothofagus* dominates, reaching almost 65% of the fossil leaves analyzed, in comparison with only 7.6% for the second most abundant morphospecies (MNHN-SGO-PB-1765, Fig. 5). A cut-off analysis of 300 samples indicates that the BDH site presents a larger diversity than at ARB. In 746 samples, the rarefaction analysis shows that the diversity at BDH totals 17 morphospecies, compared to 15 morphospecies at ARB (Fig. 6). Shannon (H) and Simpson (1 – D) index indicates low biodiversity in both localities, but BDH is higher

Table 1
Identified morphospecies in Baguales Fossil Flora.

ID MNHN	Division	Affinity (family)	Genus	Phytogeographic elements.	Oligocene Baguales Flora Fossil
MNHN-SGO-PB-1763.	Magnoliophyta (dicot)	Nothofagaceae	<i>Lophozonia</i>	Austral-Antartico	2307
MNHN-SGO-PB-1765	Magnoliophyta (dicot)	Indet dicot	–	–	286
MNHN-SGO-PB-1771.	Magnoliophyta (dicot)	Indet dicot	–	–	256
MNHN-SGO-PB-1764.	Magnoliophyta (dicot)	Myrtaceae	–	–	179
MNHN-SGO-PB-1761	Magnoliophyta (dicot)	Indet dicot	–	–	155
MNHN-SGO-PB-1769	Magnoliophyta (dicot)	Nothofagaceae	<i>Fuscospora</i>	Austral-Antartico	140
MNHN-SGO-PB-1749.	Magnoliophyta (dicot)	Indet dicot	–	–	138
MNHN-SGO-PB-1758	Magnoliophyta (dicot)	Fagaceae?	–	–	65
MNHN-SGO-PB-1762	Magnoliophyta (dicot)	Sapindaceae	<i>Llagunoa</i>	Neotropical	50
MNHN-SGO-PB-1759	Magnoliophyta (dicot)	Indet dicot	–	–	40
MNHN-SGO-PB-1753.	Magnoliophyta (monocot)	Poaceae	–	–	38
MNHN-SGO-PB-1747.	Magnoliophyta (dicot)	Berberidaceae	<i>Berberis</i>	Amplio	17
MNHN-SGO-PB-1770	Magnoliophyta (dicot)	Cunoneaceae?	–	Austral Asiatica	16
MNHN-SGO-PB-1767	Magnoliophyta (dicot)	Indet dicot	–	–	16
MNHN-SGO-PB-1748.	Magnoliophyta (dicot)	Indet dicot	–	–	12
MNHN-SGO-PB-1745.	Magnoliophyta (dicot)	Monimiaceae	<i>Peumus</i>	Endémico	5
MNHN-SGO-PB-1755.	Pteridophyta	Dryopteridaceae	<i>Polystichum</i>	–	4
MNHN-SGO-PB-1742.	Pinophyta (gymnosperm)	Podocarpaceae	<i>Podocarpus</i>	Pantropical	3
MNHN-SGO-PB-1768.	Magnoliophyta (dicot)	Indet dicot	–	–	3
MNHN-SGO-PB-1746	Magnoliophyta (dicot)	Indet dicot	–	–	3
MNHN-SGO-PB-1756.	Magnoliophyta (dicot)	Gesneriaceae	<i>Mitriaria</i>	Endémico	2
MNHN-SGO-PB-1750	Magnoliophyta (dicot)	Grossulariaceae Ribes 1	<i>Ribes</i>	Amplio	2
MNHN-SGO-PB-1743	Magnoliophyta (dicot)	Grossulariaceae, Ribes 2	<i>Ribes</i>	Amplio	2
MNHN-SGO-PB-1740.	Pteridophyta	Blechnaceae	<i>Blechnum</i>	–	2
MNHN-SGO-PB-1757	Magnoliophyta (dicot)	Fabaceae	<i>Senna</i>	Pantropical	1
MNHN-SGO-PB-1744.	Magnoliophyta (dicot)	Lauraceae	–	Pantropical	1
MNHN-SGO-PB-1741.	Pteridophyta	Dennstaedtiaceae	<i>Histiopteris</i>	–	1
MNHN-SGO-PB-1751.	Magnoliophyta (dicot)	Indet dicot	–	–	1
MNHN-SGO-PB-1760	Magnoliophyta (dicot)	Indet dicot	–	–	1

In Baguales Fossil Flora was identified 29 morphospecies: 24 morphospecies of dicotyledons, 3 pteridophytes, 1 monocotyledons, and 1 gymnosperm. At the family level, an affinity of 18 morphospecies, so that the family affinity of only 11 morphospecies could not be assigned.

Table 2
Depositional facies recognized in Río Leona Formation.

Id	Facies	Formation	General description
1	1a. Braided rivers with abandoned channels.	Río Leona.	Lithology: Fining- and coarsening-upward, medium- to coarse, greenish sandstones and conglomerates with mud clasts; mudstone and calcareous, very fine-grained sandstone lenses within sandstones.
	1b. Braided rivers proximal to ocean.	Man Aike.	Sedimentary structures: High-angle tabular and trough cross-lamination. Fossils: High content of tree trunks and poorly preserved leaf fragments; shark teeth in 1b.
2	2a. Point bars in meandering rivers.	Río Leona.	Lithology: Three types of fining-upward cycles: Medium-grained sandstone to nodular mudstone; coarse- and medium-grained sandstone to fine- and very fine-grained sandstone; coarse, clast-supported, monomictic conglomerate to fine conglomerate. Conglomerates contain very fine-grained sandstone lenses.
	2b. Point bars in meandering distributary channels.	Man Aike.	Sedimentary structures: High-angle tabular and trough cross-lamination; upper flow regime parallel lamination; rib-and-furrow structures; current ripple marks in 2a; wave ripples in 2b. Fossils: Bivalves, oysters, shark teeth in 2b, vertebrates, arthropods, tree trunks and leaves in 2a. Ichnofossils: Arenicolites, arthropod trails in 2b.
3	Subaerial flood plains.	Río Leona.	Lithology: Multicoloured mudstones with thin, grey to brown shale, reddish siltstone and fine-grained sandstone beds and lenses. Fossils: Wood fragments, leaves, pollen.
4	Overbank swamps.	Río Leona.	Lithology: Sapropelite interbedded with black mudstone. Fossils: Wood fragments and leaves.
5	5a. Crevasse splays on flood plains.	Río Leona.	Lithology: Fine- to medium-grained sandstone; quartz and chert clasts; calcareous sandstone beds with CaCO ₃ nodules in 5b.
	5b. Crevasse splays in interdistributary bays.	Man Aike.	Fossils: Tree trunks, leaves, vertebrate fragments in 5a. Bivalves, gastropods, oysters, shark teeth, leaves, tree trunks, vertebrate fragments in 5b.
6	Estuaries and interdistributary bays.	Man Aike.	Lithology: Greenish grey mudstones and grey to brown shales with thin interbeds of siltstone and fine-grained sandstone. Fossils: Wood fragments, leaves, bivalves, oysters, shark teeth.
7	Tidal channels.	Man Aike.	Lithology: Coarse- to medium-grained sandstones and clast-supported, monomictic conglomerates; beds and lenses have erosional bases; CaCO ₃ nodules. Sedimentary structures: Upper flow regime horizontal lamination; high-angle tabular and trough cross-lamination; herringbone cross-lamination in 7b. Fossils: Burnt wood fragments in 8a. Burnt wood fragments, shark teeth in 7b. Trace fossils: Skolithos in 7b.

(H = 1.75; 1 – D = 0.76) compared to ARB (H = 1.33; 1 – D = 0.54) The CHAO2 index indicates that richness is higher in BDH (41) compared to ARB (29), whereas Jackknife indicates 39.5 at BDH and 28.7 at ARB. In spite of the fact that ARB has a larger number of taxa, the

diversity and richness indexes show a decrease in comparison with BDH. This reduction in diversity is accompanied by Jaccard's similarity index of 0.24.

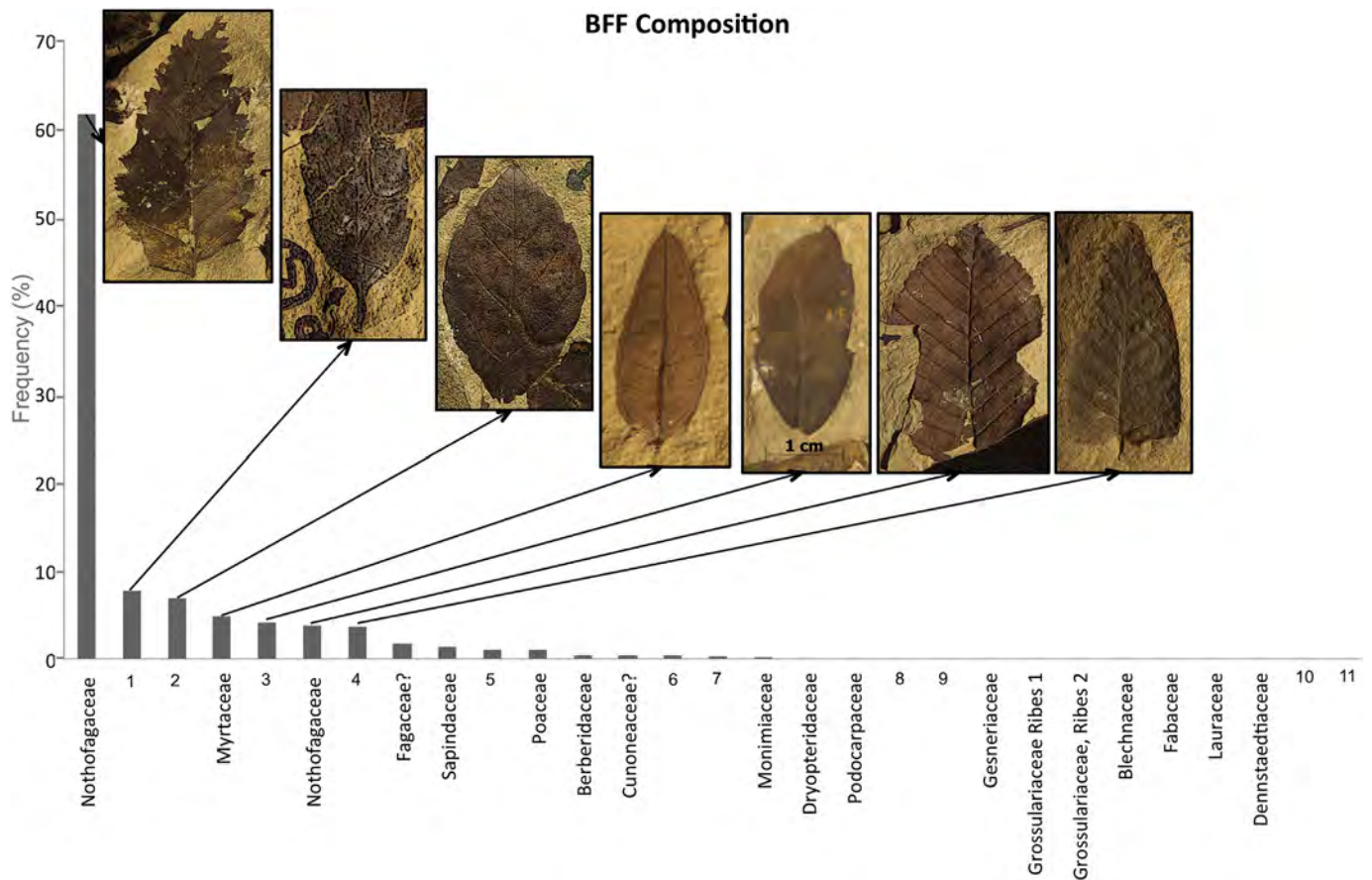


Fig. 5. Relative species abundance and composition of leaves sampled from Baguales Fossil Flora. Unidentified angiosperms: 1) NMHN-SGO-PB-1765; 2) NMHN-SGO-PB-1771; 3) NMHN-SGO-PB-1761; 4) NMHN-SGO-PB-1749; 5) NMHN-SGO-PB-1759; 6) NMHN-SGO-PB-1767; 7) NMHN-SGO-PB-1748; 8) NMHN-SGO-PB-1768; 9) NMHN-SGO-PB-1746; 10) NMHN-SGO-PB-1751; 11) NMHN-SGO-PB-1760.

4.2. Paleoclimate

The Univariate Temperature Model shows that the percentage of morphospecies with an entire margin is 21% (pE). The MAT according to the model proposed by Hinojosa et al. (2011) for South America is $26.03 * pE + 1.31 = 6.7 (\pm 2.8) ^\circ\text{C}$. On the other hand, the MAT estimation according to the model of Peppe et al. (2011) is $20.4 * pE + 4.6 = 8.9 (\pm 4.8) ^\circ\text{C}$. The Univariate Precipitation Model indicates that the mean annual precipitation according to the Hinojosa (2005) equation ($1.63 + 0.49 * \text{MLnA}$) gives an estimated MAP of 93.1 ($-89.1 + 98.1$) cm/year. The difference in the temperature and precipitation value, estimated for ARB and BDH localities does not present significant differences. Canonical Correspondence Analysis (CCA) indicates that the temperature-related variables are associated with the CCA1 axis whereas the precipitation-related variables are associated with the CCA2 axis (Fig. 7).

The estimated climatic results for the BFF are (Figs. 8, 9): Mean Annual Temperature (MAT): $9.2 (\pm 2.1) ^\circ\text{C}$; Warmest Month Mean Temperature (WMMT): $13.1 (\pm 2.9) ^\circ\text{C}$; Coldest Month Mean Temperature (CMMT): $3.7 (\pm 3.7) ^\circ\text{C}$; Number of Months with Temperatures Exceeding $10 ^\circ\text{C}$ (GROWSEAS): 9 months (± 1.3 days). The temperature range (WMMT-CMMT) of $9.4 ^\circ\text{C}$, with a relatively high seasonality gradient, shows that the climate was not equable (Axelrod et al., 1991). Thermal equality refers to a climate with a mean temperature of about $14 ^\circ\text{C}$ and a thermal variation of almost zero. As far as precipitation is concerned, the following results were obtained: Growing Season Precipitation (GSP): $82.2 (\pm 46.9)$ cm; Mean Monthly Growing Season Precipitation (MMGSP): $8.48 (\pm 5)$ cm; Precipitation During Three Wettest Months (3WET): $57.4 (\pm 19.2)$ cm; Precipitation

During Three Driest Months (3DRY): $10.2 (\pm 13.6)$ cm. The precipitation range (3WET – 3DRY) of 47.2 indicates a high seasonality where close to 70% of the rain-or snowfall was concentrated within the three wettest months.

5. Discussion

5.1. Diversity and composition

The studied palaeoflora association in the Sierra Baguales is composed of 29 morphotypes. Two morphotypes are assigned to the family Nothofagaceae, and this latter family is the most abundant at this site, comprising 65% of the total individual paleoflora, while the other 35% belongs to conifers (Podocarpaceae), other angiosperms (Myrtaceae, Fagaceae, Sapindaceae, Poaceae, Berberidaceae, Cunoneaceae, Monimiaceae, Fabaceae, Lauraceae, Grossulariaceae, Gesneriaceae), and ferns (Dryopteridaceae, Blechnaceae, Dennstaedtiaceae). Only eleven angiosperm morphotypes could not be identified to family level, despite having good preservation and distinctive characters, it was not possible to assign them to any family (Figs. 3, 5).

The composition of the BFF is dominated by subgenus *Lophozonia* and *Fuscospora* of the *Nothofagus* genus, both of which are presently microthermal subgenera in the Southern Hemisphere (Hinojosa et al., 2016). Morphologically, as far as their leaves are concerned, there is a strong similarity among the *Nothofagus* morphospecies and those of the subgenus *Lophozonia* in the BFF, in particular between *Nothofagus glauca* and *Nothofagus obliqua*. However, the assignment to any species of Nothofagaceae should ideally be accompanied by a description of reproductive characters such as flowers or fruits, or even cuticle

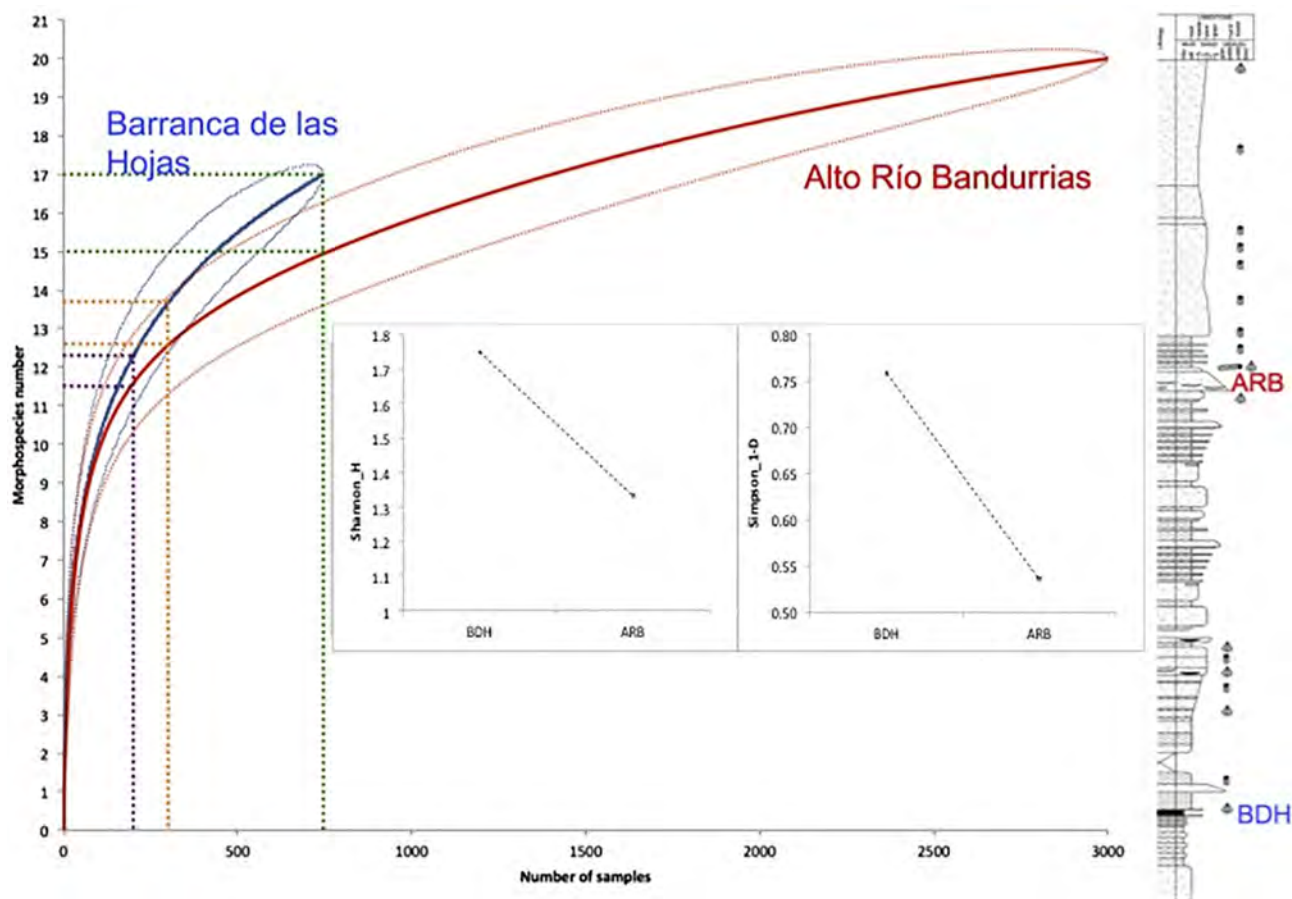


Fig. 6. Rarefaction curves for Baguales Fossil Flora, in which the number of morphospecies was derived from a sample size of 3746 fossil leaves (3000 from the ARB and 746 de from the BDH) and diversity analysis with a “cutoff analysis” at 200, 300 and 746 samples. Shannon-H and Simpson-1D diversity indexes for ARB and BDH are also shown. Stratigraphic position of Alto Río Bandurrias (ARB) and Barranca de las Hojas (BDH).

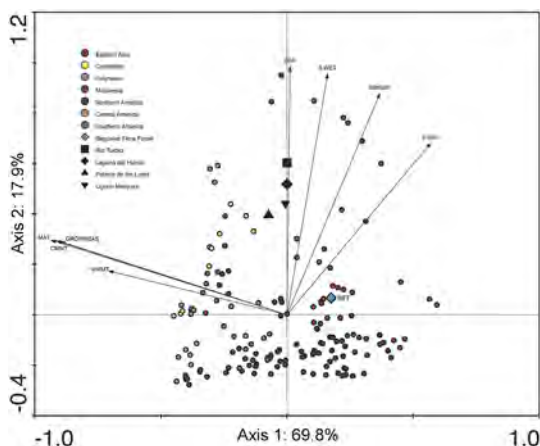


Fig. 7. The Canonical Correspondence Analysis (CCA) indicates that the temperature-related variables are associated with the CCA-1 axis and the precipitation-related variables are associated with the CCA-2 axis. CCA1: 69.8% CCA2: 17.9% and the cumulative variance of the first two axes is 87.7%, n = 161.

morphological analysis. Thus, the assignation to a specific species within the subgenera of Nothofagaceae without considering reproductive characters and cuticle analysis is very risky considering the high morphological variability in the family (Hill, 1991; Hill and Read, 1991; Hill and Jordan, 1993). For this reason, no attempt was made here to identify individual species.

The phytogeographic elements identified in the BFF correspond to Austral-Antarctic, Austral-Asian, Endemic, Pantropical and Neotropical genera, and the association can therefore be described as Mixed Palaeoflora (Romero, 1978; Hinojosa and Villagrán, 1997; Villagrán and Hinojosa, 1997, Hinojosa, 2005; Hinojosa and Villagrán, 2005; Kooyman et al., 2014). Considering the number of specimens recovered, the climatic classification of the BFF palaeoflora presents morphotypes with variable climatic requirements, in which 68.29% of the morphotypes require conditions varying from cool-cold to temperate or subtropical. Only 7.21% correspond to morphotypes with climatic requirements ranging from temperate to subtropical and tropical. Morphotypes for which no climatic classification could be established make up 24.32% of the total (Table 1).

During the Cenozoic, the fossil flora elsewhere in Patagonia registered first an increase and then a decrease in diversity according to the number of dicotyledonous morphospecies identified at each fossil locality (Fig. 10). For example, in the early Paleocene, the fossil flora of Palacio de los Loros had a diversity of 39 morphospecies (Iglesias et al., 2007), but afterwards in the early Eocene, those at Ligorio Márquez registered an increase in diversity reaching up to 55 morphospecies (Hinojosa, 2005; Hinojosa et al., 2016). A peak of diversity of morphospecies was recorded in the fossil flora of Laguna del Hunco, with 122 morphospecies (Wilf et al., 2005). However, after the early Eocene there was a clear reduction in the number of morphospecies, reaching 45 in the middle Eocene Río Turbio Formation (Hünicken, 1967). Finally, during the early Oligocene, only 24 dicotyledonous morphospecies were recorded in the BFF (Gutiérrez et al., 2017).

From the Paleocene to middle Eocene (65.5–40.4 Ma), the palaeoflora of southern South America registered a change in composition,

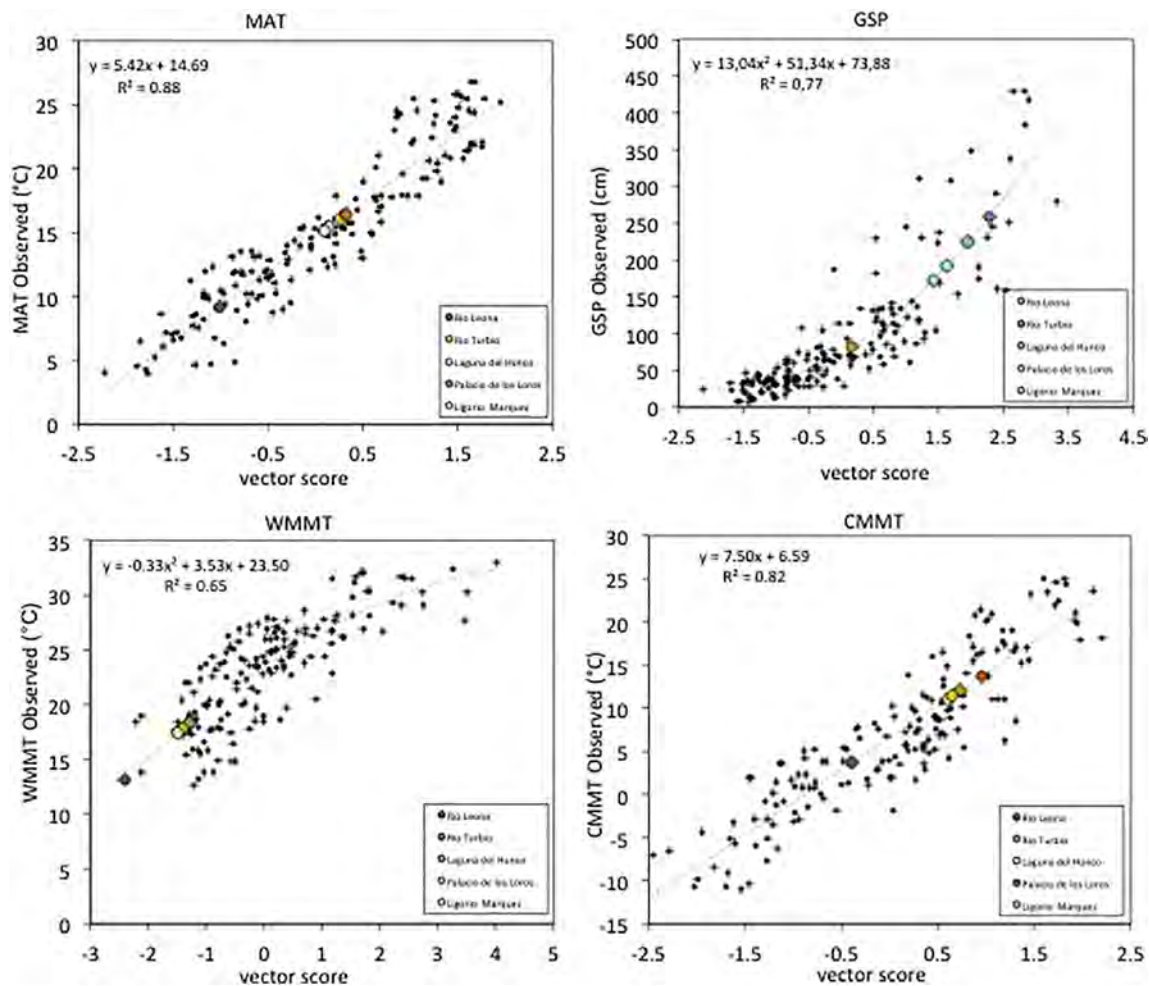


Fig. 8. Temperature results employing multivariate method for Río Leona, Río Turbio, Laguna del Hunco, Palacio de los Loros, and Ligorio Marquez. Mean Annual Temperature (MAT); Number of Months with temperature > 10 °C (GROWSEAS); Warm Month Mean Temperature (WMMT); Cold Month Mean Temperature (CMMT).

passing from Tropical Gondwana Palaeoflora to Subtropical Gondwana Palaeoflora. After the Eocene, the Subtropical Gondwana Palaeoflora were replaced by Mixed Palaeoflora, which had been migrating northward from Antarctica since the Paleocene (Dusén, 1916; Hinojosa and Villagrán, 1997, 2005; Hinojosa et al., 2006; Quattrocchio et al., 2013) and were eventually restricted to subtropical latitudes between 30° and 38°S during the Oligocene (Romero, 1978; Hinojosa and Villagrán, 1997; Villagrán and Hinojosa, 1997; Troncoso and Romero, 1998; Hinojosa, 2003, 2005; Quattrocchio et al., 2013). In the late Eocene – early Oligocene Río Guillermo Formation near Santa Cruz (Panti, 2011) and the late Oligocene Río Leona Formation of Lago Argentino (Césari et al., 2015), temperate to cold-temperate, humid climatic conditions were inferred from the palaeofloral composition (Panti, 2011; Césari et al., 2015). From the viewpoint of forest structure, the Río Leona forest canopy would have been dominated by the *Nothofagus* genus, as suggested by the high proportion of leaves of the *Nothofagus* genus in samples recovered from Río Leona (Fig. 5). Currently, species of the *Nothofagus* genus dominate or co-dominate the forests in temperate zones. Indeed, in 10 of the 12 types of forest defined for Chile, *Nothofagus* dominates the forest structure (Donoso, 1998).

The *Nothofagus* species richness during the Oligocene (Rupelian) of Río Leona is represented by only two morphospecies, being the lowest recorded since the middle Eocene (Fig. 10). During the Paleogene, the Patagonian record of fossil leaves shows that the Salamanca Formation at 45°58 'S, with a morphotype associated with *Nothofagus* (Iglesias

et al., 2007), the diversity of the genus increased progressively to reach a maximum in the middle Eocene, when seven morphotypes were recorded in Río Turbio Formation (41°S, Romero, 1978; Gandolfo, 1994; Panti, 2010). Since this maximum, during the Late Eocene, there was a decrease in diversity to only five morphotypes in Río Guillermo Formation (51°S; Panti, 2010) and three morphotypes in the Oligocene of the Río Leona Formation (49°S), specifically at the Lago Argentino locality (Césari et al., 2015). A similar pattern can be observed in the pollen record (Fig. 10), which shows maximum diversity during the middle Eocene at Río Turbio (Romero, 1978; Gandolfo, 1994), with 9 morphospecies, falling to 5–6 morphospecies during the late Eocene and Oligocene, as evidenced by the Slogget (Olivero et al., 1998; Panti et al., 2008) and Río Leona Formations (Barreda et al., 2009), respectively (Fig. 10).

The analysis of species richness and diversity in the BFF indicates a decrease in both indexes, in which the fossil leaves of the BDH, located stratigraphically at the base of the Río Leona Formation, are more diverse than those of the ARB in the upper middle part of the formation. The rarefaction analysis also demonstrates that there is a decrease in species richness in the BFF. Additionally, Jaccard's similarity index of 0.24 indicates that BDH and ARB are different, showing a turnover of species, in which the fossils of the BDH are different from those in the ARB, with the exception of the families Nothofagaceae, Myrtaceae, Grossulariaceae, and Poaceae that occur at both localities. At the BDH, Berberidaceae, Monimiaceae, Lauraceae, and Podocarpaceae were recorded, compared to Cunoneaceae, Sapindaceae, Fabaceae, and

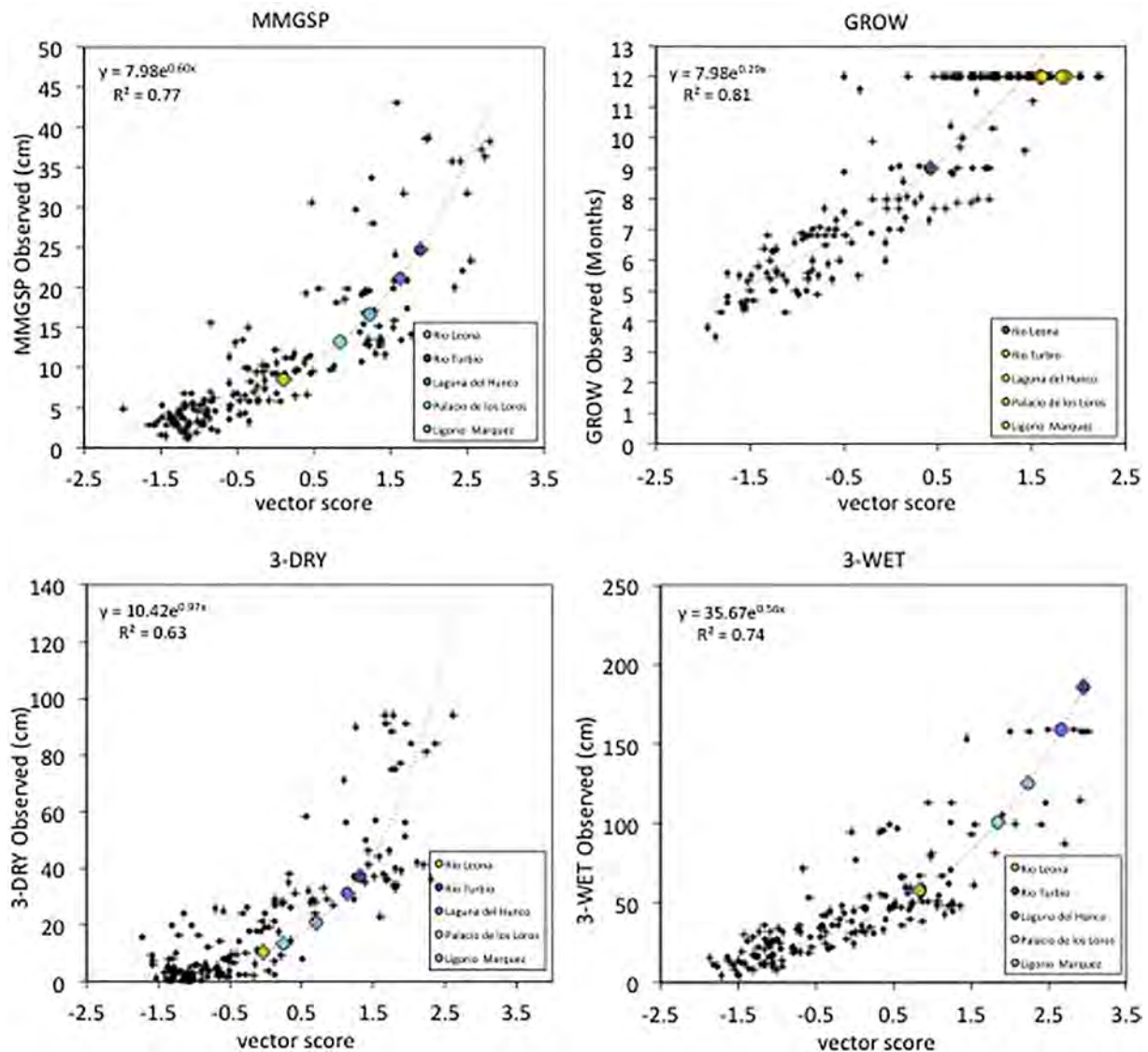


Fig. 9. Precipitation results employing multivariate method for Río Leona, Río Turbio, Laguna del Hunco, Palacio de los Loros, and Ligorio Marquez. Mean Annual Temperature (MAT); Growing Season Precipitation (GSP); Mean Monthly Growing Season Precipitation (MMGSP); Precipitation During Three Driest Months (3DRY); Precipitation During Three Wettest Months (3WET).

Gesneriaceae at the ARB. The development of the BFF, showing a decrease in diversity and changes in their composition, can be interpreted as a reaction of the vegetation to global cooling during the Oligocene that caused an increase in the temperature gradient between tropical and austral areas. This process coincided with the initiation of glaciation in Antarctica (Zachos et al., 2001; Hinojosa, 2005).

5.2. Palaeoclimate

According with our estimation, the BFF grew under a microthermal climate in the sense of Nix (1991), with a mean annual temperature estimate of 6.7–8.9 °C and an mean annual precipitation of 931 mm. Palaeotemperature estimates for the BFF demonstrate that dramatic cooling occurred in Patagonia during the Oligocene, with temperatures dropping to between 7 °C and 9 °C. The seasonal temperature variation was also high, the difference between the coldest and warmest months being 9.4 °C. This variation suggests that the climate in the BFF was not equable, but had a high seasonal variation.

As far as precipitation is concerned, the BFF registers the lowest values recorded in Patagonia during the Cenozoic, reaching 82 cm during the growing season and 93.1 cm annually. In addition, the

variation range in precipitation during the three wettest months and the three driest months was 47.2 cm, reflecting high seasonality in which nearly 70% (57 cm) of precipitation was concentrated in the wettest months, whereas the three driest months only received 10 cm of precipitation. Our palaeoclimatic data therefore suggest that the BFF experienced cool-cold and dry or sub-humid conditions during the Rupelian.

The temperature decrease recorded in the BFF during the Rupelian coincides with the Oligocene global cooling, which was registered using marine isotope data and in turn coincided with the opening of the Drake Passage and Antarctic glaciation (Zachos et al., 2001). Our data indicate the lowest precipitation recorded to date for the Cenozoic in Patagonia, falling from 200 to 240 cm during the Eocene (Hinojosa, 2005; Wilf et al., 2005; Iglesias et al., 2007) to 80–93.1 cm in the BFF during the Oligocene. This drop in precipitation is interpreted as resulting from the development of a rain shadow east of the rising Southern Patagonian Andes that blocked the humid Westerly Winds. Changes in palaeocurrent directions recorded in the BFF from the Late Cretaceous to the Miocene (Gutiérrez et al., 2017) also indicate that until the Eocene, sediments were transported towards the northwest and west, but then changed to the northeast during deposition of the

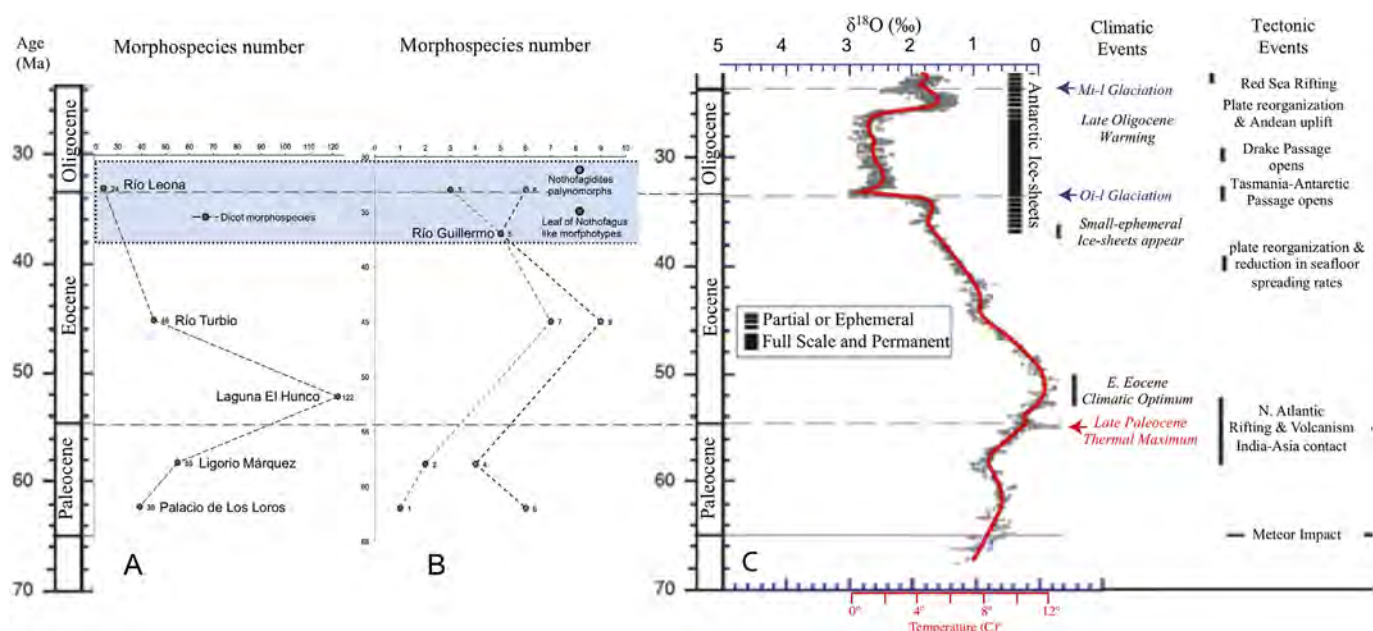


Fig. 10. Synthesis of climatic results and diversity of Patagonia during the Cenozoic; A) number of dicot for the Cenozoic in Patagonia; B) number of Nothofagidites and *Nothofagus* like morphospecies for the Cenozoic in Patagonia; C) global oxygen isotope curve (Zachos et al., 2001).

Río Leona Formation. This indicates that a major pulse of uplift in the Southern Patagonian Andes at around 34 Ma initiated the rain shadow, in contrast to the central and northern parts of Chile where this effect only became clearly manifested during the “Quechua Phase” of Andean deformation in the middle Miocene (e.g. Riccardi and Rolleri, 1980; Alpers and Brimhall, 1988; Gregory-Wodzicki, 2000; Houston and Hartley, 2003; Gutiérrez et al., 2013). As topographic forcing on climate only begins to take effect at around 1000 m (Browning, 1980), this could represent the minimum amount of uplift at the time.

Our palaeoclimatic reconstruction is the first estimate for a microthermal climate during the Rupelian, temperate conditions that dominate forest areas until today in Patagonia. In South America, according to pollen coexistence analysis, Nothofagaceae represented an ancestral, mesothermal climate with temperatures between 14 °C and 22 °C and a mean annual precipitation of 108–151 cm during the Eocene (Hinojosa et al., 2016). Independent evidence suggests that during the Oligocene, there was a marked decrease in temperature that coincided with the initiation of glaciation in the Antarctic (Barker, 2001; Zachos et al., 2001; Liu et al., 2009). Recent niche climate models also indicate that *Nothofagus* species currently occur under microthermal conditions in South America and under mesothermal conditions in tropical latitudes (Hinojosa et al., 2016). The presence of the *Nothofagus* genus in the BFF therefore suggests that it adapted to low temperature conditions between 6.7 °C and 9.2 °C during the Rupelian, constituting the first evidence that this genus supported microthermal conditions during the Oligocene in Southern Patagonia.

6. Conclusions

Statistical diversity analysis of 3746 fossil leaves, identified as the Baguales Fossil Flora of Río Leona Formation (Rupelian) in the Baguales Mountain Range of the Magallanes-Austral Basin in the Última Esperanza Province of Chilean Patagonia, presents a phytogeographic composition associated with a Mixed Palaeoflora association, dominated in this case by the Nothofagaceae family with microthermal requirements.

The response of the Baguales Fossil Flora to the global temperature drop caused an increase in the proportion of dicot morphospecies with toothed margins, whereas the decrease in precipitation resulted in

smaller leaves. Both climatic conditions generated a high-stress environment, in which Nothofagaceae adapted to microthermal conditions. This constitutes the first recorded forest dominated by Nothofagaceae under microthermal conditions in Patagonia during the Cenozoic.

The registered low temperatures coincide with a period of global marine cooling at the time, linked to the opening of the Drake Passage and the initiation of glaciation in Antarctica. On the other hand, the decrease in precipitation can be correlated with an important pulse of uplift in the Southern Patagonian Andes, which is also recorded by a change in palaeocurrent directions from northwest to northeast during the early Oligocene. This decrease in precipitation reflects the development of a rain shadow to the east of the Andes at around 34 Ma, which indicates that the Arid Diagonal developed earlier here than at lower latitudes.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.palaeo.2019.04.006>.

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