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# Did South American Mixed Paleofloras evolve under thermal equability or in the absence of an effective Andean barrier during the Cenozoic?

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## Abstract

Two hypotheses have attempted to explain the development of Mixed Paleofloras during the Cenozoic in South America. One of them postulates changes in the climatic tolerances of its component taxa and the other calls for the establishment of atmospheric thermal stability (“equable climate”) at the time these floras came into existence. We set out to test these hypotheses using leaf physiognomical analyses for eight Mixed fossil floras of the Cenozoic of Chile and Argentina. In addition to physiognomic analyses of the complete dicotyledonous flora as known from each site, we also evaluated the physiognomic significance of fossil *Nothofagus* leaves in relation to current Chilean species of the genus. Our results suggest that fossil *Nothofagus* leaves have a broader climatic envelope relative to the extant species. This divergence could be accounted by differences in their respective climatic tolerances. We postulate that the Mixed Paleoflora evolved in a subtropical climate that extended as far south as 40°S, with relatively warm temperatures and high annual rainfall with little seasonal variation. This climatic scenario is possible only with a much-reduced Andean massif, which would have permitted the spillover of moisture of easterly origin to the Pacific Andean slopes.

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## 1. Introduction

Four paleofloras have been recognized during the Cenozoic in southern South America: Neotropical, Mixed, Antarctic and Subtropical (Hinojosa and Villagrán, 1997; Romero, 1978, 1986; Troncoso and Romero, 1998; Volkheimer, 1971). Their estab-

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lishment and subsequent transitions have been linked to major tectonic and climatic events, the most salient of which are: the breaking apart of western Gondwana, Antarctic glaciations, onset of the Humboldt current and Andean orogeny (Hinojosa and Villagrán, 1997). The floristic composition characteristic of the current forest communities of southern South America would already have been differed at the end of the Tertiary. However, deep and repeated changes occurred in the patterns of distribution of the forests of the south of South America during the cycles glacial–interglaciales of the Quaternary, being favored the expansion of the woody temperate–colds taxa as *Nothofagus* and Coniferous and being negatively affected the woody floras with warmer requirements (Villagrán, 2001; Villagrán et al., 2004).

Among the Paleofloras described, Mixed Paleofloras stand out because of their broad temporal and spatial distribution. Defined by Romero (1978, 1986) as a forest formation composed of taxa from different “ecological requirements” and phytogeographic sources, it contains current both Neotropical (e.g. *Myrceugenia* and *Escallonia*) and Austral Antarctic (*Laurelia* and *Eucryphia*) floristic regions. South American Mixed Paleofloras first appeared in Antarctica, at the Paleocene/Eocene boundary (~55 Ma) (Dusén, 1916). They spread into South America during the Eocene, occupying the entire region south of 30°S latitude. During the Oligocene, they were restricted to the subtropical regions of Chile–Argentina, later occupying the Pacific coast of central Chile during the Miocene (Hinojosa, 1996; Hinojosa and Villagrán, 1997; Romero, 1978, 1986; Troncoso, 1991; Troncoso and Romero, 1998).

### 1.1. Hypothesis about South American Mixed Paleofloras

South American Mixed Paleofloras were interpreted at first as a taphonomic artifact in which several vegetation types from different altitudinal belts were preserved in a single sedimentary unit (Dusén, 1916; Menéndez, 1971; Volkheimer, 1971). Yet the sustained temporal and spatial persistence of these Paleofloras, found along a wide array of depositional environments spanning >23 million years, led Romero (1978) to propose his hypothesis

of in situ evolution unique to South America, formed by relict Cretaceous lineages enriched by (1) the cold–temperate elements arriving from Antarctica, (2) warm elements that originated in the Neotropics and (3) a strictly endemic element that originated in southern South America. The coexistence of these elements, which today occupy different climatic zones, led Romero (1978) to postulate that the floristic elements of these fossil flora have had different ecophysiological requirements (or tolerance) relative to their modern counterparts. More recently, Troncoso and Romero (1998) proposed that the prevalence of a subtropical climate analogous to current subtropical mesothermal climate, according with Köppen’s definition (Köppen, 1936), could explain this mixture of phytogeographic elements.

Quite a different perspective was put forward by Axelrod et al. (1991), who proposed that thermally homogeneous climates over extended periods during the Cenozoic set the stage for the co-occurrence of floristic elements with differing ecophysiological tolerances. Essential in this argument is the persistence of mild temperatures (~14 °C) with little or no annual variation. He developed an index termed “equability” ( $M$ ). High values of this index ( $M=100$ ) correspond to climates with a mean annual temperature (MAT) of 14 °C and a thermal amplitude of 0 °C during the annual cycle (Axelrod, 1992). At present, there are several different regions around the world which are close to thermal equability ( $M>50$ ), according to Axelrod’s (1992) definition. Examples include coastal California, Mexico, island New Guinea, region east of the Himalayas, New Zealand and eastern Australia. All of these regions today have forests characterized by mixed floras (Arroyo et al., 1995; Axelrod, 1992; Axelrod et al., 1991). In some of these, same regions also occur mixed floras during the Paleogene (Truswell, 1993).

### 1.2. Reappraisal of the problem

Based on the operational definition of equability, searching modern analogue for past Tertiary scenarios, Hinojosa (2003) calculated  $M$  indexes using meteorological data from coastal Chile (Fig. 1). The results indicate high values of thermal equability ( $M>60$ ) for almost the entire length of the country (Hinojosa, 2003), a region that encompasses hyper-

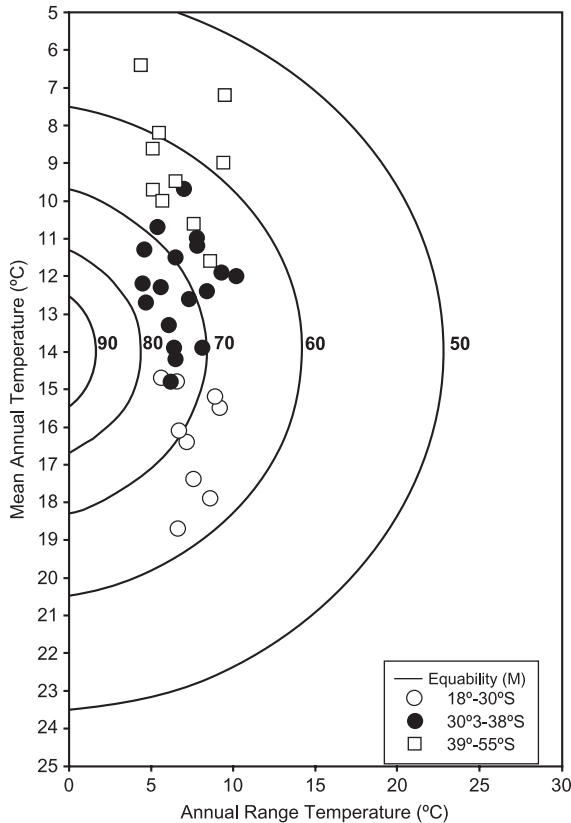


Fig. 1. Nomogram of equability according Axelrod (1992). Equability ( $M$ ) was calculated using climatic stations from the Chilean coast, between  $18^{\circ}\text{S}$  and  $55^{\circ}\text{S}$ . Annual range temperature was obtained such as difference among mean annual warm temperature and mean annual cold temperature.  $M=30-109*\log((14-\text{mean annual temperature})^2+(1.46+0.366*\text{annual range temperature})^2)$ .

arid and arid plant formations north of  $30^{\circ}\text{S}$ , sclerophyllous and deciduous *Nothofagus* forests between  $30^{\circ}\text{S}$  and  $38^{\circ}\text{S}$ , to the floristically diverse temperate rainforests distributed south of  $40^{\circ}\text{S}$  (Schmithüsen, 1956). The phytogeographic composition of these different formations is also heterogeneous. The arid formations found north of  $30^{\circ}\text{S}$  are dominated by Neotropical elements, whereas the hyperhumid formations south of  $44^{\circ}\text{S}$  are characterized by the predominance of Subantarctic elements. The area of Central Chile ( $30\text{--}44^{\circ}\text{S}$ ) features a blend of both Neotropical and Subantarctic elements, and was defined by Schmithüsen (1956) as transitional between the Antarctic and Neotropical Flora Kingdoms in South America.

The most symmetrical contributions of Neotropical and Antarctic elements are found within the transitional zone between Mediterranean and temperate climates of South–Central Chile ( $36\text{--}43^{\circ}\text{S}$ ) (Villagrán, 1995; Villagrán and Hinojosa, 1997). Thus, the proportion of Neotropical and Endemic elements increases north of  $36^{\circ}\text{S}$ , whereas Austral–Antarctic elements increase south of  $40^{\circ}\text{S}$ . A canonical correspondence analysis of this pattern versus latitude and associated climatic variables reveals three major groups (Fig. 2): (1) floras north of  $30^{\circ}\text{S}$ , (2) floras distributed between  $30^{\circ}\text{S}$  and  $41^{\circ}\text{S}$ , and (3) floras south of  $41^{\circ}\text{S}$ . Mean annual temperature and summer precipitation (JFM) are the main drivers affecting this pattern. The first group is found in the arid and dry portion of the diagram, whereas the third group lies in the extreme humid and cold portion of the diagram. The second group falls near the intersection of both axes. According to Van Husen (1967), the region between  $30^{\circ}\text{S}$  and  $41^{\circ}\text{S}$  corresponds to two climatic zones: a temperate rainfall zone with episodically dry summers and a Mediterranean zone, with wet winters and a regular dry summer season. The southern limit of the Mediterranean zone lies at  $38^{\circ}\text{S}$  and constitutes the poleward extent of the subtropical vegetation and climate regimes.

In this study, we attempt to explain the development of Mixed Palefloras in the Cenozoic of South America using univariate and multivariate paleoclimate model estimates relating fossil leaf physiognomy to modern data set. Two central hypotheses will be assessed:

- (1) If Mixed floras developed under “equable” temperature (sensu Axelrod), that meaning low thermal amplitude and mean annual temperatures around  $14^{\circ}\text{C}$  ( $M>50$ ), and a homogeneous humid regime without seasonal variation of moisture, then leaf physiognomical analysis of the fossil floras should indicate similar values of both mean annual and mean annual range temperature and both mean annual and summer precipitation for all Mixed fossil floras, even for those from different latitudes and time periods.
- (2) If ecological tolerances of the fossil taxa were different from their modern relatives, the climatic parameters associated with the fossil leaf physiognomy should differ significantly from the parameters deduced from their modern descendants.

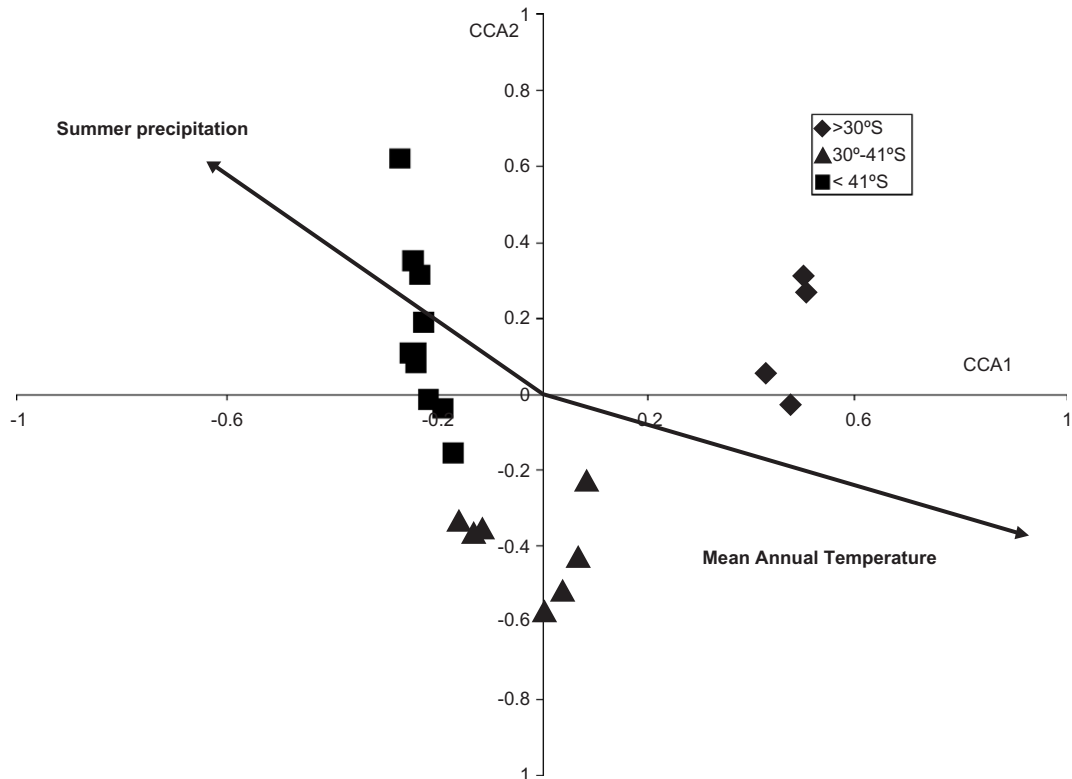


Fig. 2. Canonical correspondence analysis of the phytogeographical distribution along a latitudinal gradient in Chile (Hinojosa and Villagrán, 1997). The first two canonical axes accumulate 97% of the total variance. Mean annual temperature is correlated with axes 1 with  $r=88\%$ . Precipitation of three consecutive driest months (summer precipitation in Southern Hemisphere) are correlated with axes 2 with  $r=54\%$ . Association among phytogeographical elements and environmental variables was significant with  $p<0.001$ , Monte Carlo test, and  $r=0.674$ ,  $p<0.0001$ ,  $\alpha=0.001$ , Mantel Test (Hinojosa, 2003).

Hence, the purpose of this work is to test both hypotheses based on an analyses of leaf physiognomy for eight Mixed Paleofloras of the Cenozoic of South America. We estimated modern precipitation and temperature based on present-day models that correlate leaf physiognomy and climate from different regions of the world.

## 2. Materials and methods

### 2.1. Mixed fossil floras (Table 1)

All of the taphofloras used in this study have been classified as Mixed Paleofloras in the literature. They range from the lower Eocene to the upper Miocene (53–15 Ma) and have been collected in localities from

Chile and Argentina, from 33°S to 51°S latitude (Table 1, Fig. 3). Leaf characters were measured directly on specimens from collections at the Laboratorio de Palinología of the Universidad de Chile and Universidad de Buenos Aires; the paleobotany collections for the Museo Nacional de Historia Natural at Santiago, Chile; Museo Bernardino Rivadavia, Buenos Aires, Argentina; and the Museo de Paleobotánica at the Universidad de Concepción. We also used numerical values obtained from fossil descriptions found in the literature.

### 2.2. Modern leaf physiognomic analyses

This type of analyses is based on the correlation between woody dicotyledonous leaf morphology and climatic variables that take into account temperature

Table 1

Mixed fossil floras considered for physiognomic analysis (1=literature; 2=Lab. Ecología y Sistemática Vegetal, Universidad de Chile collection; 3=Museo de Historia Natural, Santiago, Chile collection; 4=Museo Argentino de Historia Natural, Buenos Aires, Argentina collection; 5=Lab. Paleobotánica Universidad de Buenos Aires, Argentina collection; 6=Museo Paleontológico, Universidad de Concepción, Chile collection)

Taoflora	Geologic age	Dates (Ma)	Latitude (°S)	Phytogeographic character	No. morpho-taxa	Authors	Collections
Navidad-Boca Pupuya	Middle–upper Miocene	?	33°57'	Mixed/ <i>Nothofagus</i>	27	Martínez-Pardo (1990), Troncoso (1991), Hinojosa and Villagrán (1997), Troncoso and Romero (1998)	3
Navidad- Goterones	Lower Miocene	23 (Sr)	33°57'	Mixed/ <i>Nothofagus</i>	28	Martínez-Pardo (1990), Troncoso (1991), Hinojosa and Villagrán (1997), Troncoso and Romero (1998), Gregory (pers. comm.)	3
Cerro Las Aguilas	Upper Oligocene	26–23 (Ar/Ar)	33°19'	Mixed/ <i>Nothofagus</i>	42	Hinojosa (1996), Hinojosa and Villagrán (1997), Selles and Hinojosa (1997), Hinojosa (unpublished)	2
Ñirihuau	Upper Eocene/ lower Oligocene	?	41°15'	Mixed/ <i>Nothofagus</i>	33	Berry (1928), Firori (1931, 1940), Romero (1978, 1986), Troncoso and Romero (1998)	1
Rio Turbio	Middle Eocene	?	51°33'	Mixed/ <i>Nothofagus</i>	72	Hünicken (1967), Romero (1978, 1986), Troncoso and Romero (1998)	1
Laguna del Hunco	Lower Eocene	52 (Ar/Ar)	42°27'	Mixed	30	Berry (1925), Romero (1978, 1986), Mazzoni et al. (1991), Troncoso and Romero (1998)	1, 4, 5
Quinamávida	Lower Eocene	?	35°7'	Mixed	29	Troncoso (1991), Troncoso and Romero (1998)	3
Pichileufu	Lower Eocene	?	41°7'	Mixed	120	Berry (1938), Romero (1978, 1986), Troncoso and Romero (1998)	1, 5

This table displays the geographic coordinates, phytogeographic character, geologic age (with absolute and/or relative dates), authors and number of taxa analyzed (all woody dicotyledonous) per flora.

and moisture. The percentage of leaves with smooth margins, for example, is positively correlated to mean annual temperature, whereas leaf size is correlated with mean annual precipitation (MAP). This modern relationship constitutes the analogue for inferring paleoclimate based on an association of fossil leaves (Bailey and Sinnott, 1916; Dilcher, 1973; Dolph and Dilcher, 1979; Kovach and Spicer, 1996; Sinnott and Bailey, 1915; Wiemann et al., 1998; Wilf, 1997; Wing and Greenwood, 1993; Wolfe, 1971, 1979, 1993).

By using the modern relation between climate and vegetation, many numeric models have been proposed that estimate temperature and moisture based on fossil leaves. These methods are based on univariate and

multivariate analyses of modern leaf traits with their respective climates. Leaf data from fossil leaf assemblages are then incorporated into the regression equations obtained. The most widely used data set is Climate–Leaf Analysis Multivariate Program (CLAMP) developed by Wolfe (1993) based on a systematic collection of plant and climate data from North America and Asia. This data set has been updated in three successive versions. The newest version available, CLAMP3, has been updated with climate-leaf data from 17 localities from Bolivia (Gregory-Wodzicki, 2000) and Chile (Hinojosa, 2003, 2005), and was used in this paper. This updated version we call CLAMP3 SA. For our analyses, we have used a more restricted version, CLAMP3B SA

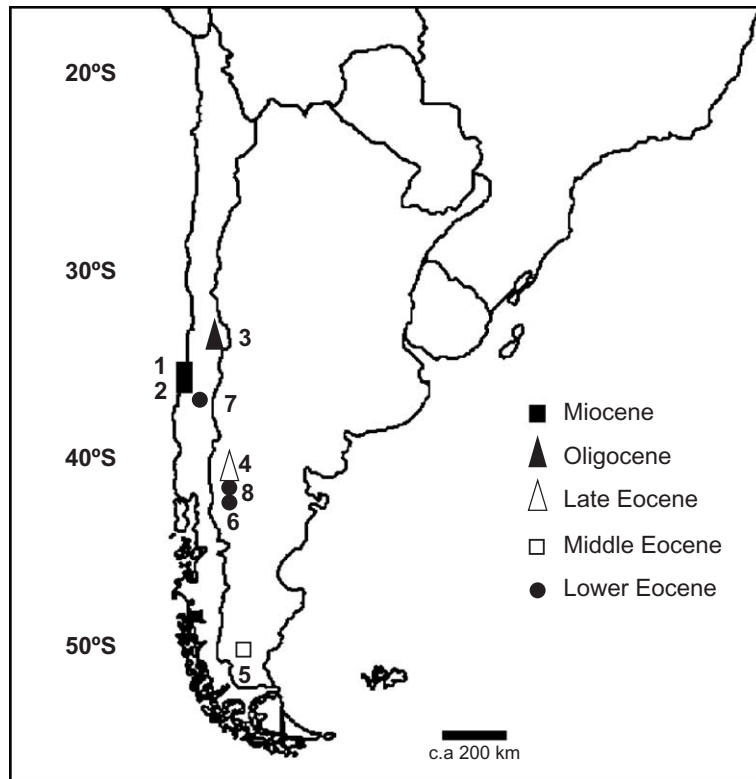


Fig. 3. Geographical and stratigraphic distribution of mixed fossil floras considered in this study. 1: Boca Pupuya, 2: Goterones-Matanza, 3: Cerro Las Aguilas, 4: Ñirihuau, 5: Rio Turbio, 6: Laguna del Hunco, 7: Quinamávida, 8: Pichileufu.

(161 locations), which excludes the data from the coldest and driest localities (Wilf, 1997; Wing and Greenwood, 1993), where attention is drawn to the exclusion of sites with coldest mean month temperatures  $< 2^{\circ}\text{C}$  (Wing and Greenwood, 1993), values not registered in South American climates, which are mostly under oceanic influence (Schwerdtfeger, 1976).

Leaf traits were measured directly on four of the taphofloras included in this study. On the other four taphofloras, foliar data were gathered from the primary literature, some of which (Laguna del Hunco and Pichileufu) were further augmented by direct measurements at the paleobotanical collections at Buenos Aires, Argentina.

Greenwood (1992) and Gregory-Wodzicki and McIntosh (1996) suggested the need to incorporate the error generated by subestimation when smaller leaves (those in modern leaf litter) are not included

versus overestimation generated from using only the larger leaves from the canopy. When fossil leaves were abundant, at Cerro Las Aguilas for example, if they could be classified in either adjacent size class, they were placed into both classes. This correction was not applied to museum collections which, unfortunately, are “collection-biased”, i.e. the specimens usually include well preserved, rare and/or large fossils, and exclude fragmentary and/or more common fossils (Gregory-Wodzicki et al., 1998; Taggart and Cross, 1990). Finally, Wilf (1997) suggest to incorporate the binomial error generated by different number of morpho-taxa present in a fossil flora. These errors were calculated to mean annual temperature estimate and are giving in the text. When the binomial error was lesser than the standard error of the estimate, then standard error was used (Wilf, 1997; Wilf, pers. comm.).

### 2.3. Univariate methods

Leaf margin analysis (LMA) carry out by linear regressions for MAT were calculated by using the percentage of non-toothed leaves and the climate values CLAMP3B SA data set. MAP was obtained by a linear regression of mean of natural log leaf areas (MLnA), versus climate values. The value for MLnA was determined for each CLAMP3B SA data set after the equation of Wilf et al. (1998) and using the CLAMP size classification system (Gregory-Wodzicki, 2000). These are summarized in Table 2, which also displays the equations obtained, determination coefficients and model standard error. Paleotemperatures and precipitation were obtained by replacing the measured values (% non-toothed leaves, MLnA) for the eight fossil floras studied into the equations in Table 2.

### 2.4. Multivariate methods

These methods are, on a theoretical level, more adequate for characterizing the relationship between leaf traits and environmental variables, especially when one considers that these characters could differentially respond to one or more variables (Gregory-Wodzicki, 2000). Multiple regressions (Jacobs, 1999; Wiemann et al., 1998; Wing and Greenwood, 1993) and gradient analyses are among the most commonly used methods. The latter frequently use either indirect techniques, such as principal component analysis and correspondence analysis (Jacobs, 1999; Wolfe, 1993), or direct techniques such as canonical correspondence analysis (Gregory-Wodzicki, 2000; Herman et al., 1996; Wiemann et al., 1998; Wolfe, 1995). In this work, we use a CCA ordination of CLAMP3B SA data set, using 31 leaf traits and varying values for temperature and precipitation. CCA ordinations were

performed using CANOCO v.4 for Windows (ter Braak and Smilauer, 1998). We applied CCA to eight different climate variables as per the CLAMP3B SA data set. The environmental variables used in the CCA analysis were: mean annual temperature, cold-month mean temperature (CMMT), warm-month mean temperature (WMMT), length of the growing season, i.e. those month with mean temperatures  $\geq 10$  °C (GSP), mean growing season precipitation (MGSP), mean monthly growing season precipitation (MMGSP), precipitation of the three consecutive wettest month (or mean precipitation of wet season, MPW) and precipitation of the three consecutive driest months (or mean precipitation of dry season, MPD).

Environmental variables were calculated by non-linear regressions between the orthogonal projection of each data set site on the corresponding vector and the climate variables for each fossil flora locality.

### 2.5. Physiognomic analysis of *Nothofagus*

We analyzed 29 leaf traits for both modern Chilean (10 species) and fossil (27 species) of *Nothofagus*. These include tooth type, leaf area, type of leaf apex and base, length/width ratio and shape. Modern leaf traits were gathered from species dwelling along the Coastal Range of Chile, from 32°S to 55°S lat. (Parque Nacional La Campana, Reserva Nacional Los Ruiles, Reserva Nacional Los Queules, Parque Nacional Nahuelbuta and Monumento Nacional Alerce Costero). *Nothofagus* values were obtained by digitizing both freshly collected material and specimens from the Herbario de la Universidad de Concepción, Chile. A total of 890 *Nothofagus* leaves were analyzed. Leaf area and length/width ratio were measured directly on 5–20 leaves per sample with Sigmascan v.5. Other characters were obtained

Table 2  
Univariate models used to obtain climatic estimate of tertiary fossil floras from southern South American

Model	Equation	R <sup>2</sup>	Standard error	Data set
Mean annual temperature	MAT=3.25+0.25*% non-tooth	0.9	2.1 °C	CLAMP3B SA (n=161)
Mean annual precipitation	Ln(MAP)=1.63+0.49*MLnA	0.6	Ln(0.5) cm	CLAMP3B SA (n=161)

CLAMP data set by Jack Wolfe and modified by Gregory-Wodzicki (2000) and Hinojosa (2003, 2005). All equations are significant with  $p < 0.001$ .

directly from the aforementioned collections and samples. Correspondence analysis was then used to compare morphological variation between modern and fossil *Nothofagus* from Mixed fossil floras (ter Braak and Smilauer, 1998). The axes positions obtained from the correspondence analysis were then incorporated into a cluster analysis with results presented as a dendrogram (Fig. 14). The significance level ( $p < 0.05$ ) of this dendrogram was calculated by bootstrap analysis (Manly, 1991), using the morphological score from the first four axes of the correspondence analysis and 1000 permutations were carried out.

### 3. Results

#### 3.1. Mean annual temperatures

Regression analysis using leaf margin analysis shows that the proportion of non-toothed species is correlated significantly with MAT ( $F: 1097.9$ ,  $P < 0.001$ ) with a determination index of 0.9 and a standard error of 2.1 (Table 2). Regression analysis using the multivariate model also indicate a significant equation ( $F: 602.98$ ,  $P < 0.001$ ) with a determination index of 0.9 and a standard error of

2.1 °C. We can thus affirm that the temperature estimates obtained are equivalent among these two models, but they are consistently higher for the univariate model. Figs. 4 and 5 show the MAT during the Cenozoic for the univariate (Fig. 4) and multivariate (Fig. 5) models when applied to the CLAMP3B SA data set.

The results obtained from the leaf margin analysis (Fig. 4) indicate that the three Mixed fossil floras without *Nothofagus* from the early Eocene (45–46 Ma): Quinamávida, Pichileufu and Laguna del Hunco, have relatively high mean annual temperatures that oscillate between 19.3 ( $\pm 2.2$ ) and 20.6 ( $\pm 2.1$ ) °C. These later declined slightly during the middle to late Eocene (40–43 Ma) at Rio Turbio and Ñirihuau (Mixed Paleofloras with *Nothofagus*), which demonstrate temperatures between 17.7 ( $\pm 2.1$ ) and 18.4 ( $\pm 2.2$ ) °C. A tendency towards lower temperatures is observed from the beginning of the Oligocene to the lower Miocene (23–29 Ma), culminating with values between 16.6 ( $\pm 2.1$ ) and 16.9 ( $\pm 2.4$ ) °C (3 °C lower than the temperatures observed for the early Eocene) at Cerro Las Aguilas and Navidad-Goterones, localities with Mixed Paleofloras with *Nothofagus*. Finally, mean annual temperatures rose markedly during the lower to upper Miocene (23–10 Ma), reaching values of 25.6 ( $\pm 2.1$ ) °C at Navidad-Boca Pupuya, the

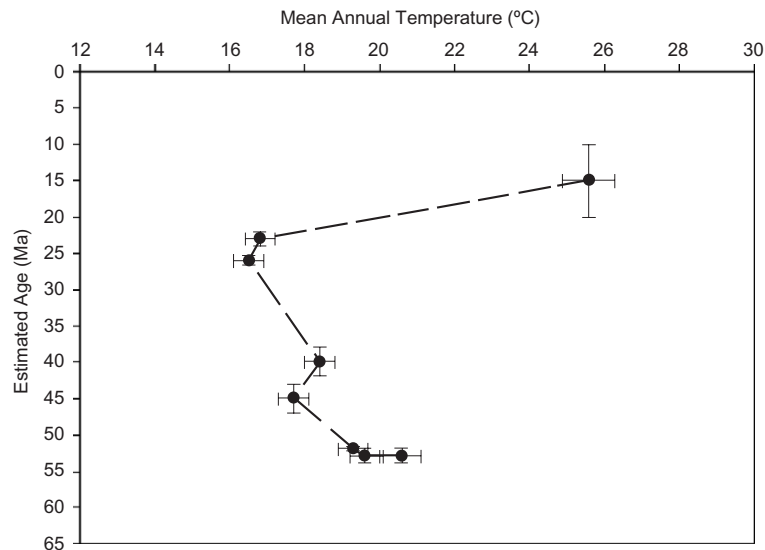


Fig. 4. Mean annual temperature estimated from mixed fossil floras, based on univariate model. MAT bars are 95% confidence interval.



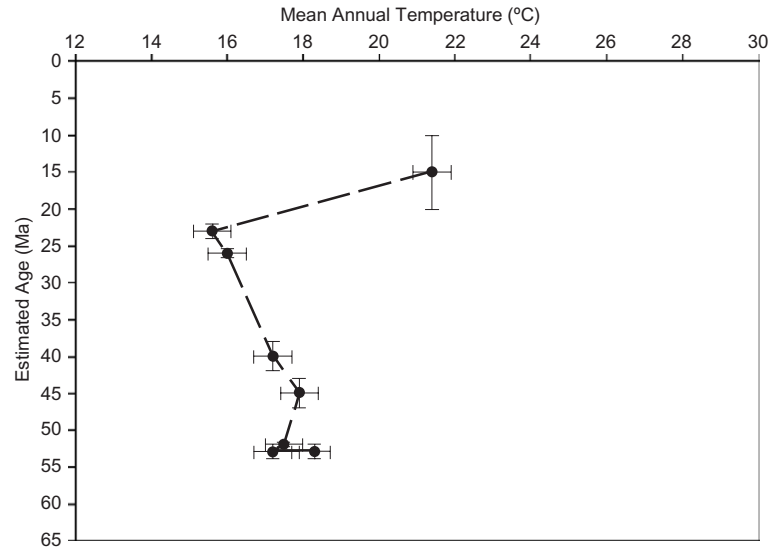


Fig. 5. Mean annual temperature estimated from mixed fossil floras, based on multivariate model. MAT bars are 95% confidence interval.

highest observed for any Mixed fossil floras during the Cenozoic.

Results from our multivariate model (Fig. 5) indicate similar tendencies to those obtained from the univariate model, although with slightly lower temperatures. Thus, for the three Mixed taphofloras without *Nothofagus* from the early Eocene as well as for a Mixed fossil floras with *Nothofagus* from the middle Eocene, we obtained MATs between 17.2 ( $\pm 2.3$ ) and 18.3 ( $\pm 2.1$ ) °C. From the end of the Eocene to the lower Miocene, Mixed fossil floras with *Nothofagus* from Ñirihuau, Cerro Las Aguilas and Navidad-Goterones display a sustained decline in MATs culminating with minimum values of 15.6 ( $\pm 2.4$ ) °C at Goterones, some 2.3° C lower than the

MATs observed during the middle Eocene. Between 23 and 10 Ma, the Navidad-Boca Pupuya taphoflora shows a substantial temperature increase, reaching 21.4 ( $\pm 2.1$ ) °C, almost 6 °C higher than those observed during the lower Miocene. These elevated temperatures have no equivalent among the other Mixed fossil floras and are more closely associated with the Paleocene Neotropical Paleofloras (Hinojosa, 2003, 2005).

### 3.2. Cold-month mean temperature

Estimates for CMMT from the multivariate model (Table 3) exhibit a determination index of 0.8 °C and a standard error of 3.8 °C. Eocene Mixed fossil

Table 3

Multivariate model used to obtain climatic estimates of tertiary fossil floras from southern South America

Model	Equation	$R^2$	Standard error	Data set
Mean annual temperature	$MAT = -8.1 + \exp(3.1 + (0.24 * MATv))$	0.9	2.1 °C	CLAMP3B SA (n=161)
Warm-month mean temperature	$WMMT = 23.6 + 3.42 * WMMTv - 0.4 * WMMTv^2$	0.5	3.3 °C	CLAMP3B SA (n=161)
Cold-month mean temperature	$CMMT = -35.2 + \exp(3.7 + (0.2 * CMMTv))$	0.8	3.8 °C	CLAMP3B SA (n=161)
Mean growing season precipitation	$MGSP = 75.5 * \exp(0.53 * MGSPv)$	0.8	42.6 cm	CLAMP3B SA (n=161)
Mean precipitation of dry season	$MPD = 17.5 * \exp(0.7 * MPDv)$	0.6	15.3 cm	CLAMP3B SA (n=161)
Mean precipitation wet season (three consecutive wettest month)	$MPW = -32.6 + \exp(4.3 + 0.3 * MPWv)$	0.7	19.8 cm	CLAMP3B SA (n=161)

CLAMP data set by Jack Wolfe and modified by Gregory-Wodzicki (2000) and Hinojosa (2003, 2005). All equations are significant with  $p < 0.001$ . MATv, WMMTv, CMMTv, MGSPv, MPDv and MPWv are environmental vectors from CCA analysis.

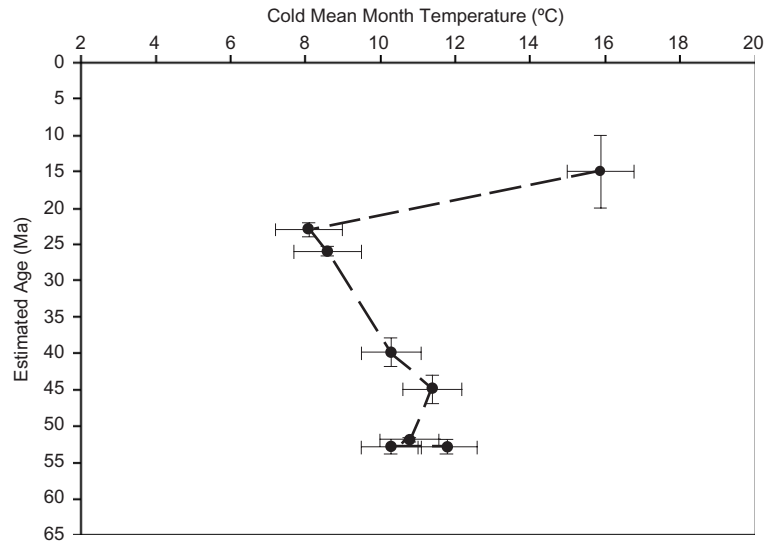


Fig. 6. Cold mean month temperature estimated from mixed fossil floras, based on the multivariate model. CMMT bars are 95% confidence interval.

floras from five localities exhibit CMMT estimates of 10.3 and 11.8 °C for the CLAMP3B SA model (Fig. 6). Considerably lower values are indicated by Mixed fossil floras with *Nothofagus* from the upper Oligocene to the lower Miocene, with minimums between 8.1 ( $\pm 3.8$ ) and 8.6 ( $\pm 3.8$ ) °C. These later increases at Navidad-Boca Pupuya from the lower to

upper Miocene, culminating with values of 15.9 ( $\pm 3.8$ ) °C.

### 3.3. Warm-month mean temperatures

Determination index obtained from the multivariate model for WMMT was of 0.5 and standard

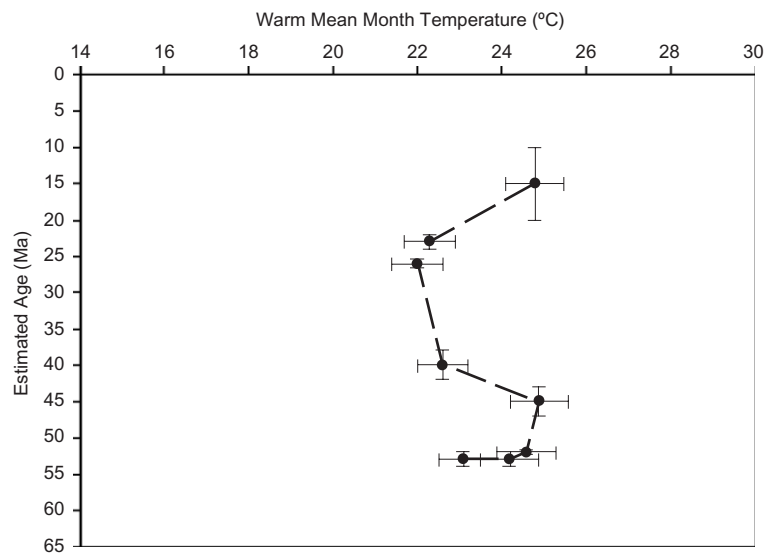


Fig. 7. Warm mean month temperature estimated from mixed fossil floras, based on the multivariate model. WMMT bars indicate 95% confidence interval.

error of 3.3 °C (Table 3). However, and in contrast with the results for CMMT, no large differences were observed for this parameter among the Mixed fossil floras studied (Fig. 7). The one exception is the temperature descent observed at Cerro Las Aguilas during the upper Oligocene, with estimates of 22.0 ( $\pm 3.3$ ) °C, in stark contrast with 24.8 ( $\pm 3.3$ ) °C in the upper Miocene (Navidad Boca-Pupuya) and 24.9 ( $\pm 3.3$ ) °C during the middle Eocene (Río Turbio).

### 3.4. Thermal oscillation

The thermal amplitude observed for all the Mixed fossil floras can be appreciated in Fig. 8, where we have graphed the mean minimum and maximum temperatures as well as the difference between these parameters. The annual thermal oscillation indicates very little variation from the lower Eocene to the lower Miocene. During the upper Miocene, however, an abrupt decrease in thermal amplitude occurred at Navidad-Boca Pupuya. This is also displayed, albeit not as dramatically, at the Pichileufu taphoflora from the lower Eocene. In both cases, this decrease between

the annual extreme temperatures is given by an increase in the minimum temperatures. Thus, the thermal optima during the Paleocene/Eocene boundary and during the middle Miocene were chiefly caused by an increase in minimum temperatures, therefore thermal amplitude decreased and thermal equability increased.

### 3.5. Mean annual precipitation

Mean annual precipitation was calculated using simple regressions combined with CLAMP3b SA data set. A determination coefficient of 0.6 with a standard error of Ln 0.5 cm was obtained (Table 2).

For our data set, MAP decreases throughout the Cenozoic (Fig. 9). A maximum MAP of 166.3 (–65.4, +107.9) and 193.7 (–76.2, +125.7) cm occurs at the beginning of the Eocene for the Pichileufú and Laguna del Hunco Mixed fossil floras without *Nothofagus*, respectively. Estimates from the Quinamávida locality of the same period, however, are lower. From the middle Eocene to lower Miocene, MAP drops dramatically to values of 152.4 (–60, +98.8), 103.1 (–40.6, +66.9) and 76.2 (–30.0, +49.4)

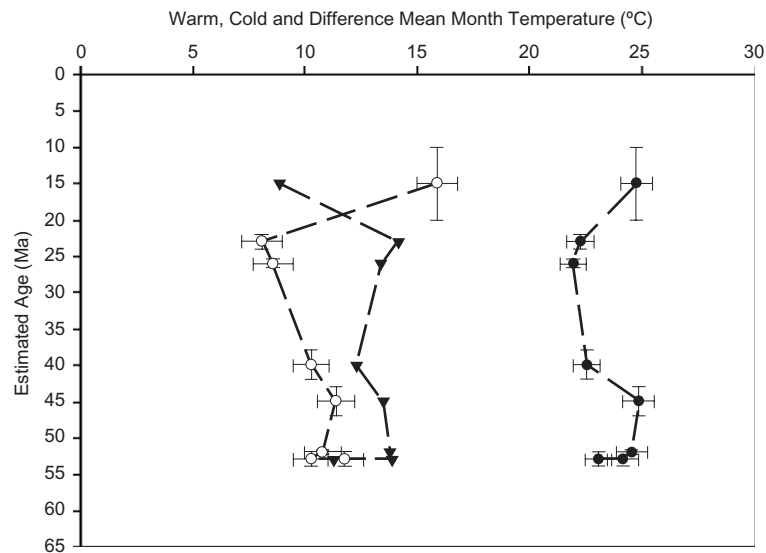


Fig. 8. Warm, cold and difference mean month temperature estimates. Symbols are: warm temperature (square), cold temperature (circle) and differences between them (triangle).

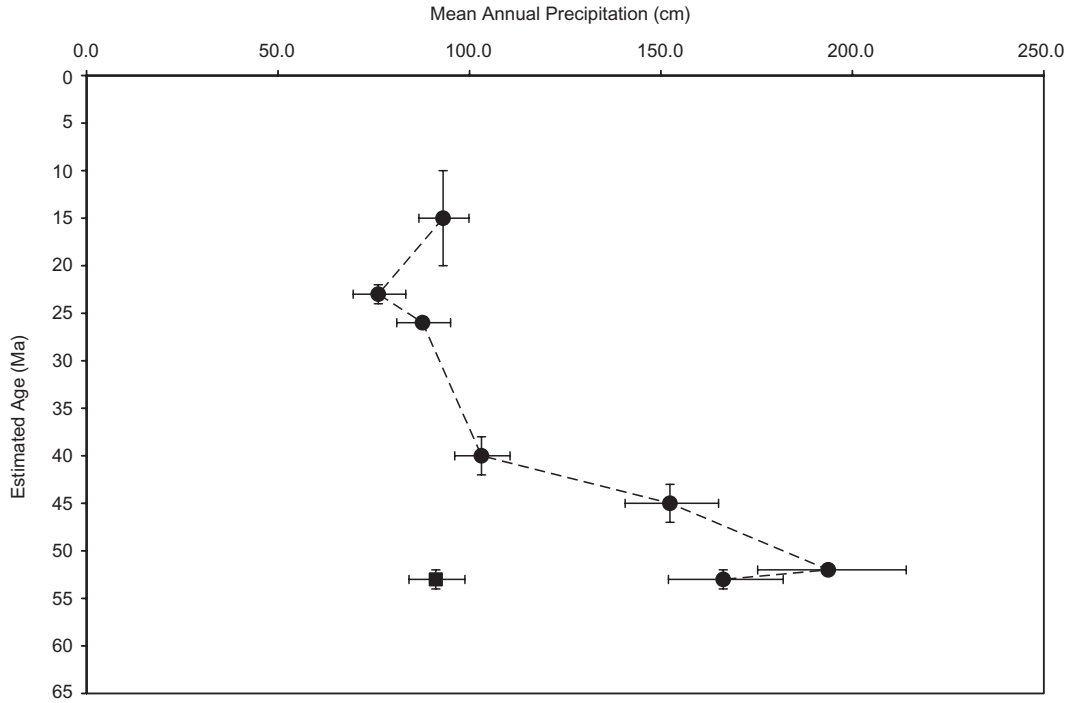


Fig. 9. Mean annual precipitation estimated from mixed fossil floras, based on univariate model. MAP bars are 95% confidence interval.

cm at the three localities of Mixed fossil floras with *Nothofagus*. This trend reverts at the Boca Pupuya member of the Navidad Formation, with MAP

estimates of 93.1 (−36.6, +60.4) cm. These estimates are close equivalents to those from the Mixed fossil floras of the middle Eocene.

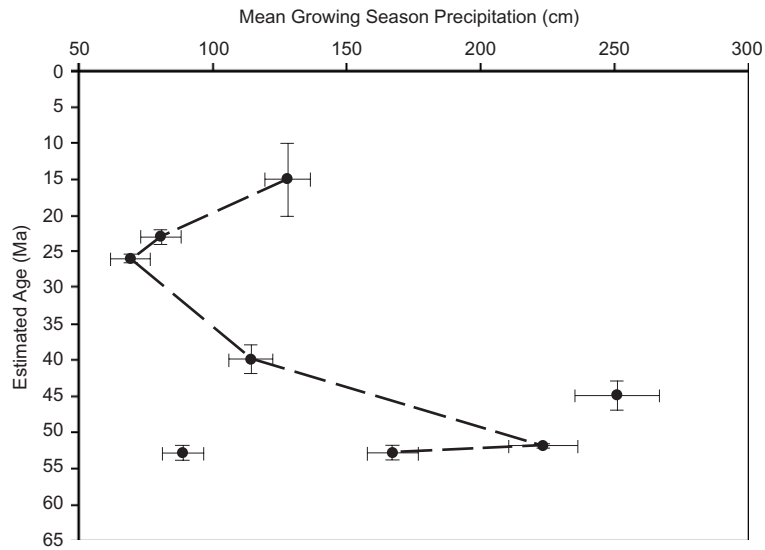


Fig. 10. Mean growing season precipitation estimated from mixed fossil floras. MGSP bars are 95% confidence interval.

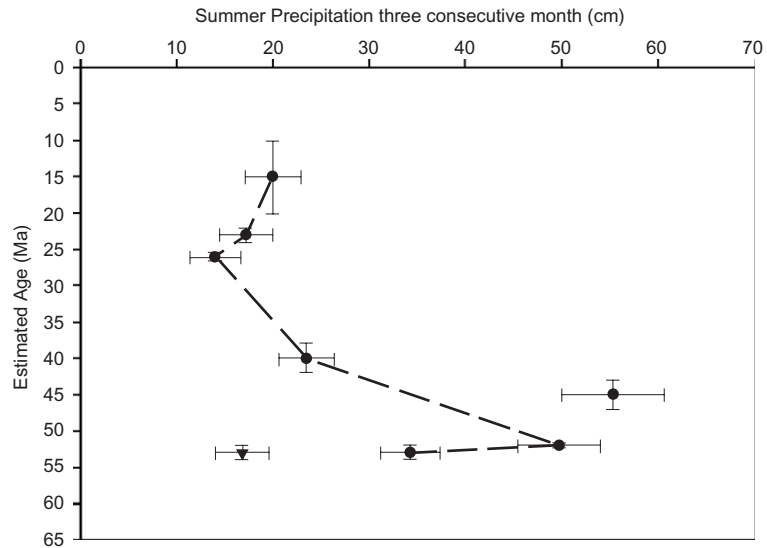


Fig. 11. Three consecutive driest months (summer precipitation) based on estimates from mixed fossil floras of southern South America. MDP bars indicate 95% confidence interval.

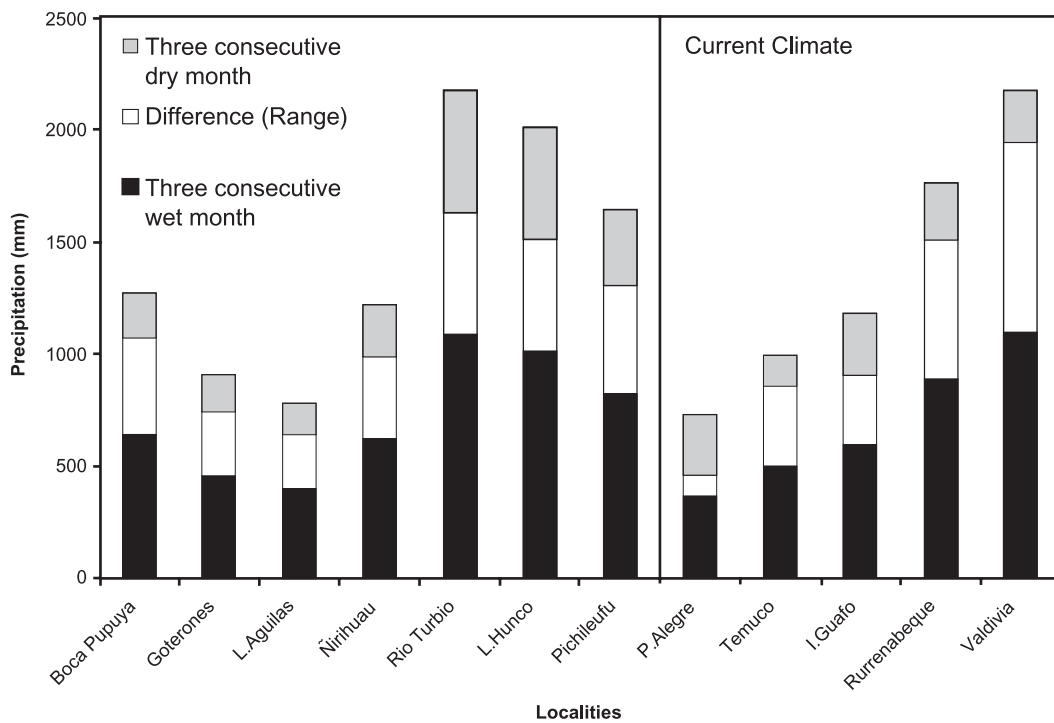


Fig. 12. Wet and dry season precipitation and precipitation range based on estimates from mixed fossil floras. Right side shows the equivalent quantity at the some current climatic stations from South America.

### 3.6. Mean growing season precipitation

MGSP was estimated with the multivariate model (Table 3). The determination index obtained with CLAMP3B SA was 0.8 and standard error is 42.6 cm (Table 3).

As with MAP, estimates for MGSP show an overall decline throughout the Cenozoic (Fig. 10). Early Eocene Mixed fossil floras without *Nothofagus* display estimates of 167.3 and 223.7 cm. The Quinamavida taphoflora again presents anomalously low values (88.8 ( $\pm 42.6$ ) cm). Mixed fossil floras with *Nothofagus* from Río Turbio of the middle Eocene have values of 251.4 ( $\pm 42.6$ ) cm. Beginning at the lower Miocene at Navidad-Goterones, we again observe an increase in the MGSP, which culminates in Navidad-Boca Pupuya, with a maximum of 128.0

( $\pm 42.6$ ) cm. These estimates of MGSP are similar to those obtained from the Ñirihuau taphoflora of the middle to upper Eocene and are close to half the amounts obtained for early Eocene Mixed fossil floras.

### 3.7. Mean precipitation of the dry season

The estimates obtained to MPD (the three driest months) had a determination coefficient of 0.6 and standard errors of 15.3 cm (Table 3, Fig. 11). Again, the maximum values were obtained from the lower Eocene Mixed fossil flora without *Nothofagus* from Pichileufu and Laguna del Hunco and from the middle Eocene Mixed fossil flora with *Nothofagus* at Río Turbio. Estimates obtained run from 34.3 ( $\pm 15.3$ ) to 55.4 ( $\pm 15.3$ ) cm. Estimates from Quina-

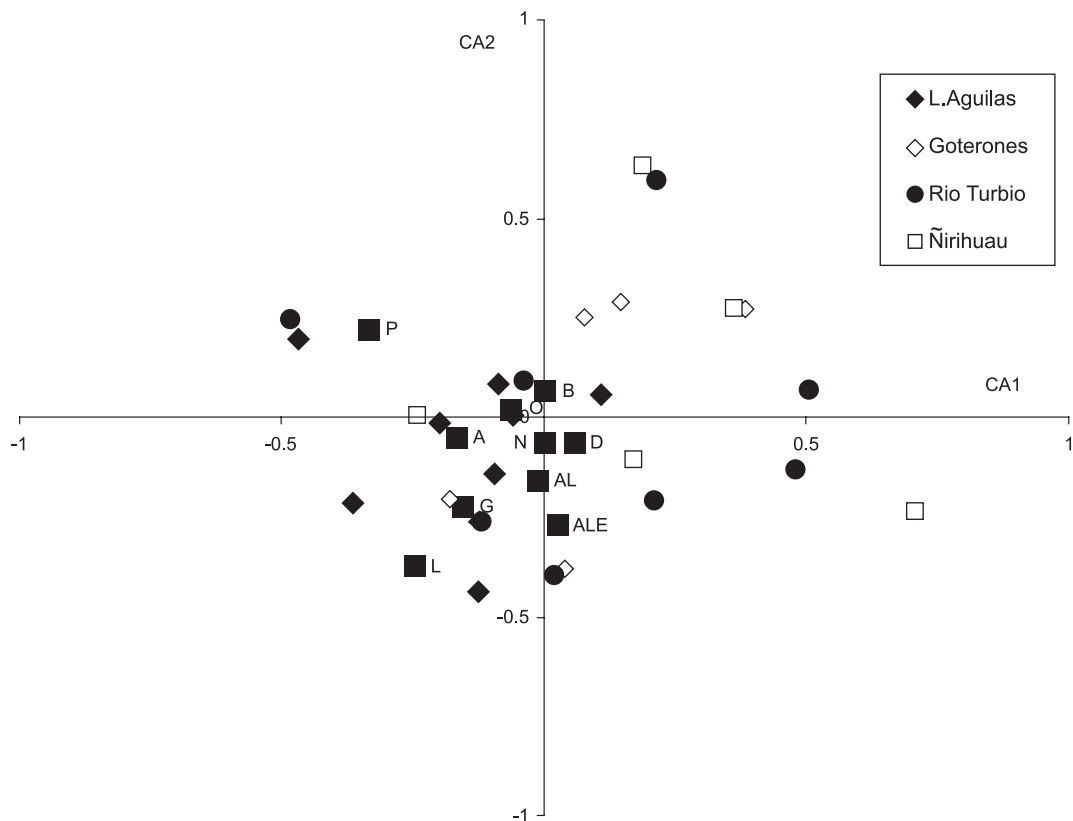


Fig. 13. Correspondence analysis diagram, considering foliar-physiognomic characters of current (black square) and fossils (others symbols) *Nothofagus*. P=*N. pumilio*, B=*N. betuloides*, O=*N. obliqua*, A=*N. antarctica*, D=*N. dombeyi*, AL=*N. alpina*, G=*N. glauca*, ALE=*N. alessandrii*, L=*N. leonii*.

mávida are again below those obtained from other coetaneous Mixed fossil floras with 16.8 ( $\pm 15.3$ ) cm. MPD quickly drops in the middle Eocene, culminating at Ñirihuau with estimates of 23.5 ( $\pm 15.3$ ) cm. This declining trend eases up during the Oligocene, with values of 14.0 ( $\pm 15.3$ ) cm at Cerro Las Aguilas. MPD estimates obtained from the two members of the Navidad Formation during the Miocene increase slightly to 17.2 ( $\pm 15.3$ ) and 20.0 ( $\pm 15.3$ ) cm.

### 3.8. Precipitation seasonality

By comparing the estimates obtained for the three wettest months versus those from the three driest

months, we have plotted the differences among each these different parameters (Fig. 12). We have also included several modern southern South American climates for comparison as well. The highest values for both the driest and wettest seasons come from the lower to middle Eocene. Equivalent values are observed today at Valdivia, along the temperate rainy coast of Chile and at Rurrenabeque station, located along the Cordillera Oriental of the Andes (López and Aceituno, 1998). Seasonality, however, is more pronounced at the modern localities, which tend to have drier summers. Precipitation estimates for the Oligocene Mixed fossil floras are much lower, although the seasonal contrast remains the same as

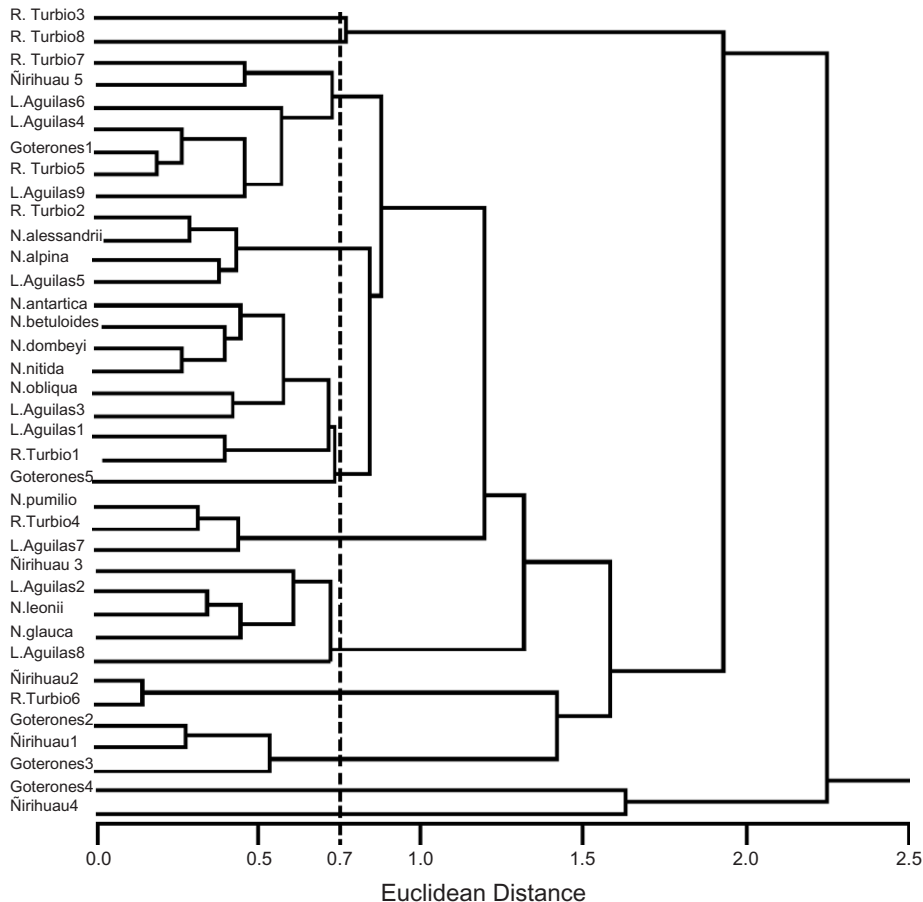


Fig. 14. Euclidean distance dendrogram based on morphological score of the correspondence analysis of Fig. 13 (first four axes). Broken line at 0.7 was obtained by bootstrap analysis ( $\alpha$ : 0.05). 60% of fossil *Nothofagus*, from Mixed Paleofloras, has larger distance than those groups contained both current and fossil *Nothofagus*.

the previous period. The climate at the weather station of Temuco, located at the interface between the Mediterranean and temperate climate regimes of Chile, is the closest modern hydrological analogue to these fossil floras.

### 3.9. Physiognomic analysis of the genus *Nothofagus*

Within a correspondence analysis of the leaf traits of fossil and extant species of *Nothofagus*, the first two axes explain about 30% of the total variance (Fig. 13). In general, the clustering close to the origin of the living species of the genus clearly denotes a restricted range of environmental requirements when compared to the fossil species. *Nothofagus pumilio*, a southern Chilean forest species that lives in temperate cold regions close to treeline, tends to group with some of the fossil *Nothofagus* found in Mixed fossil floras from the middle Eocene to upper Oligocene. Thus, the extreme left portion of axis one can be associated with colder temperatures whereas the extreme right portion, where several fossil taxa of the genus from the lower to middle Eocene are found, can be associated with warmer temperatures. Along the same lines, the southernmost hygrophilous species *N. betuloides* plots near the origin whereas the more drought resistant taxa, *N. glauca*, *N. leonii* and *N. alessandrii* plot along the extreme lower portion of axis two. Thus, this axis can be associated with humidity and precipitation. Several fossil species of *Nothofagus* from the upper to middle Eocene plot near the positive extreme of axis two, which would imply very wet conditions with no modern analogue.

We constructed a dendrogram (Fig. 14) based on a cluster analysis that considered the positions of the extant and fossil species of *Nothofagus* in terms of the first four axes of correspondence (53.2% of the total variance). Our dendrogram agrees with what we have previously stated in that approximately 60% of the fossil taxa have Euclidean distances greater than those expected by random (0.7). This is beyond the range displayed by the modern species (0.2–0.7). The species *N. pumilio* again displays an anomalous pattern, falling within the clade formed by the colder Mixed fossil floras with *Nothofagus* of the upper Eocene and Oligocene.

## 4. Discussion and conclusion

### 4.1. Did the Mixed Paleofloras evolve as a response to thermal equability?

According to Axelrod et al. (1991), one of the major explanations for the large temporal and spatial range occupied by the Mixed fossil floras during the Cenozoic of South America was thermal equability, thus mean mild temperatures with low thermal amplitude. Our leaf physiognomic analysis of eight Mixed fossil floras concurs with the concept of thermal equability of Axelrod et al. (1991). In particular, the development of Mixed fossil floras (lower Eocene to the Miocene) occurred under relatively homogenous mean annual temperatures which, despite a slight negative trend, do not differ by more than 2.7 °C (multivariate analysis) or 3.7 °C (univariate analysis). The mean annual averages exhibit values, ranging between 15 and 20 °C. The mean temperature of the warmest month is also nearly constant among the Mixed fossil floras studied. The mean temperature of the coldest month is also equivalent among the Mixed fossil floras without *Nothofagus* from the beginning of the Eocene and for the Mixed fossil floras with *Nothofagus* from the upper Oligocene–lower Miocene. Thus, thermal amplitude experienced very little variation for during this period.

A different pattern arises during the middle to upper Miocene, however. Analyses of the Navidad-Boca Pupuya Mixed fossil floras gave mean annual temperatures over 20 °C in both the multivariate and univariate models. These temperatures are 6–9 °C higher than those obtained for the taphoflora of the underlying unit Goterones (lower Miocene) as well as the other Mixed fossil floras from earlier periods. In fact, these temperatures are only observed in Paleocene Neotropical Paleofloras (Hinojosa, 2003, 2005). The extreme temperatures observed in these floras are also substantially higher, especially winter temperatures. Thus, the thermal contrast of the Boca Pupuya floras was considerably less than for the other Mixed fossil floras during the Cenozoic, as can be gleaned from the decrease in the thermal oscillation index. These floras are thus even more equable, according to Axelrod's concept, than the other Mixed floras.



The thermal equability index calculated for all the Cenozoic Paleofloras oscillates between 50 and 60 (Fig. 15). Despite this thermal homogeneity, the Mixed Paleofloras are floristically highly distinct between those with and without *Nothofagus* during the Eocene, and those dominated by *Nothofagus* from the upper Oligocene to the lower Miocene. We also cannot thermally differentiate the Mixed Paleoflora from the Paleocene Neotropical Paleoflora, or

from Eocene/Oligocene Antarctic Paleoflora, or from the Subtropical Paleoflora of the middle Miocene (Hinojosa, 2003, 2005). Similarly, the equability index calculated for modern coastal Chile along a large latitudinal gradient between 30°S and 55°S is over 60, which does not reflect the diverse floras that occupy this region today (Fig. 1). Because all of these highly diverse floras and Paleofloras fall within thermal equability, this parameter cannot be invoked to explain the presence of Mixed fossil floras throughout most of the Cenozoic.

#### 4.2. Did the Mixed Paleofloras evolve under a humid regime with little seasonal variation of moisture?

We also considered the possibility that the Mixed Paleofloras evolved under a homogeneous humid climate without seasonal contrast, analogous as the climate with thermal equability proposed by Axelrod. Contrary to that expected from hypothesis one, the precipitation estimates obtained show: (1) the precipitation estimates obtained show a marked negative trend throughout the Cenozoic. The high values observed for the Mixed fossil floras without *Nothofagus* from the lower Eocene contrast with the lower values estimated for the Mixed fossil floras with *Nothofagus* from the upper Oligocene to lower Miocene. This is reflected in a 40% decrease in MAP, a 36% decrease in MGSP and up to a 30% decrease in MPD. (2) No significant variations were observed between the wet and dry seasons for the Paleogene to lower Neogene fossil floras studied as the net decrease occurred in both seasons. (3) Seasonal contrast in precipitation is observed in the middle and upper Miocene fossil floras.

The trend of decreasing precipitations, however, reverted during the middle to upper Miocene at Boca Pupuya. As with temperature, the precipitation estimates are significantly higher being equivalent to those calculated for the upper Eocene taphofloras at Ñirihuau. In contrast, estimates for MPD are only slightly higher at Boca Pupuya. Thus, mean an increase in precipitation seasonality at this locality, with very wet winters yet drier summers. One possibility is that this increase in seasonality was due to a higher rainfall shadow generated by the

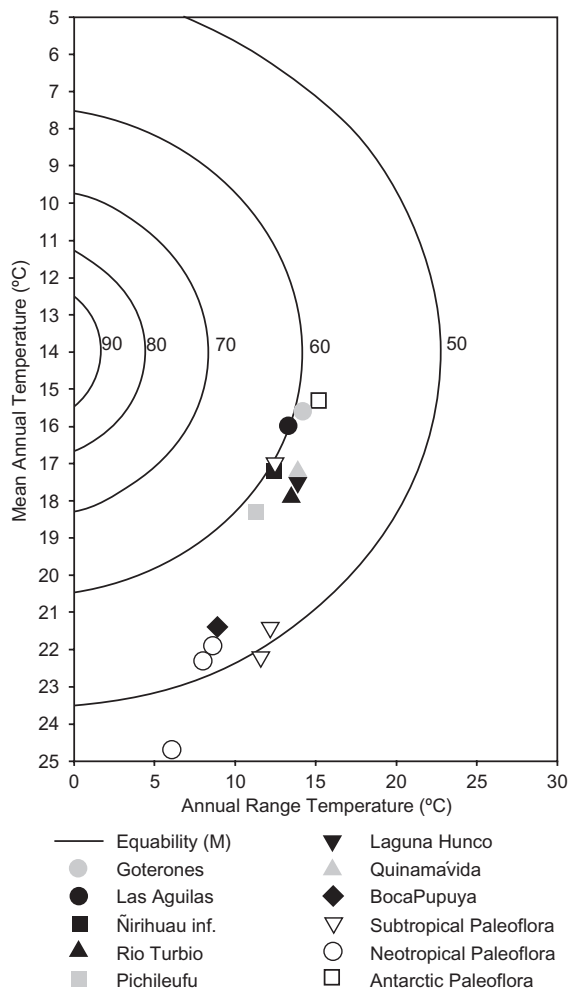


Fig. 15. Nomogram of equability ( $M$ ) according Axelrod (1992). Closed symbols: different Mixed Paleofloras from South America. Open symbols: other paleofloras from southern South America, according Hinojosa and Villagrán (1997) and Hinojosa (2003).  $M=30-109*\log((14-\text{mean annual temperature})^2+(1.46+0.366*\text{annual range temperature})^2)$ .

Andes, which during the upper Miocene had already reached half of their present elevation (Gregory-Wodzicki, 2000).

Hence, these results argue against precipitation stability associated with thermal equability as an explanation for the Mixed Paleofloras. It is possible that these floras evolved under a climate regime with no modern analogue.

#### 4.3. Incorporating paleotopography and the role of the Andes

When confronted by the enigma posed by the South American Mixed Paleofloras, perhaps an actualistic approach is not the way to resolve this puzzle. The explanation could reside in the singular topography present during for most of the Cenozoic of southern South America. A much reduced or virtually absent Andes Cordillera would eliminate the double rainshadow this produces on the two major climate systems (tropical easterlies and extratropical westerlies), which dominate the continent today. Such a scenario would be particularly helpful in understanding the evolutionary history of the vegetation over a large part of this region, in particular the subtropical band between

30°S and 40°S, which extended further south in the past. Modern-day climate is characterized in this region by a strong east–west contrast, with dry summers produced by the Andes blocking moisture from the Amazon brought over by the easterlies. It is only by the waning and northward displacement of the subtropical south Pacific anticyclone during the winter that westerly moisture reaches the Pacific coast of central–southern Chile, effectively generating the modern-day Mediterranean climate (Aceituno, 1988; Lenters and Cook, 1995; Miller, 1976; Van Husen, 1967). This also generates a strong north–south precipitation gradient, as the westerly influence grows weaker towards the north. In contrast, the eastern slope of the Andes is summer wet and winter dry, with a pronounced and reversed northeast to southwest precipitation gradient (Lenters and Cook, 1995; Schwerdtfeger, 1976).

During most of the Cenozoic, the Andes had much lower elevations and would not have exerted as strong an influence on these climate systems as they do today. Only during the upper Miocene, the average elevation was half of that at present (Gregory-Wodzicki, 2000). Thus, it was clearly possible that for most of the Paleogene and much

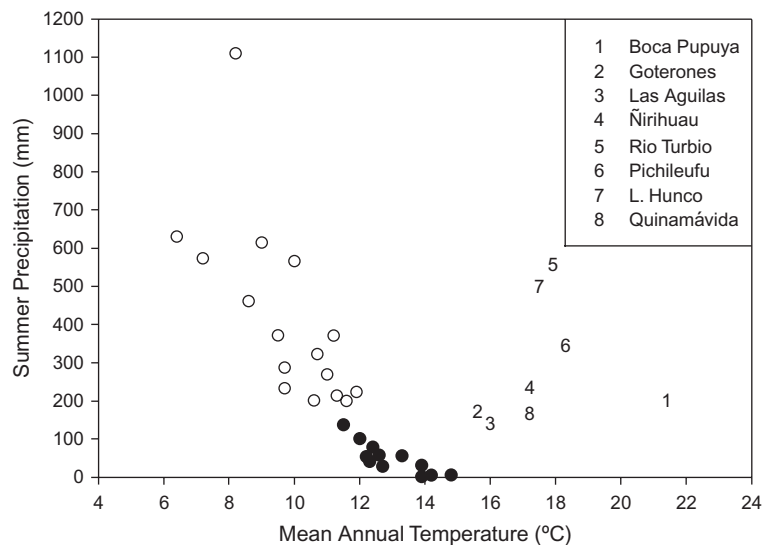


Fig. 16. Relationship between mean annual temperature and summer precipitation (three consecutive driest months: January, February, March). Black circle: Chilean meteorological station between 30°S and 41°S. Open circle: Chilean meteorological station between 42°S and 55°S. Numbers: Mixed Paleofloras.

of the Neogene (until at least the middle Miocene), precipitation across the subtropical belt would have been brought by both the easterlies and the westerlies. The latitudinal position of this belt has also changed through time, reaching at least  $46^{\circ}\text{S}$  during the thermal optimum of the Paleocene/Eocene (Hinojosa, 2003, 2005; Troncoso et al., 2002). Thus, the subtropical belt during the Cenozoic would have offered optimum conditions for the development of Neotropical lineages adapted to summer rains, and Australasian or Austral-

Antarctic lineages adapted mostly to winter rains. The coexistence of all these elements was largely due to the elevated temperatures present for most of the Cenozoic, as well as an overall increase in precipitation due to the presence of two wet seasons during the year. Global circulation models run under the absence of mountains and with different latitudinal temperature gradients, both of which force precipitation over South America, indicate that the climate regime proposed above was quite possible during the Cenozoic (Lenters

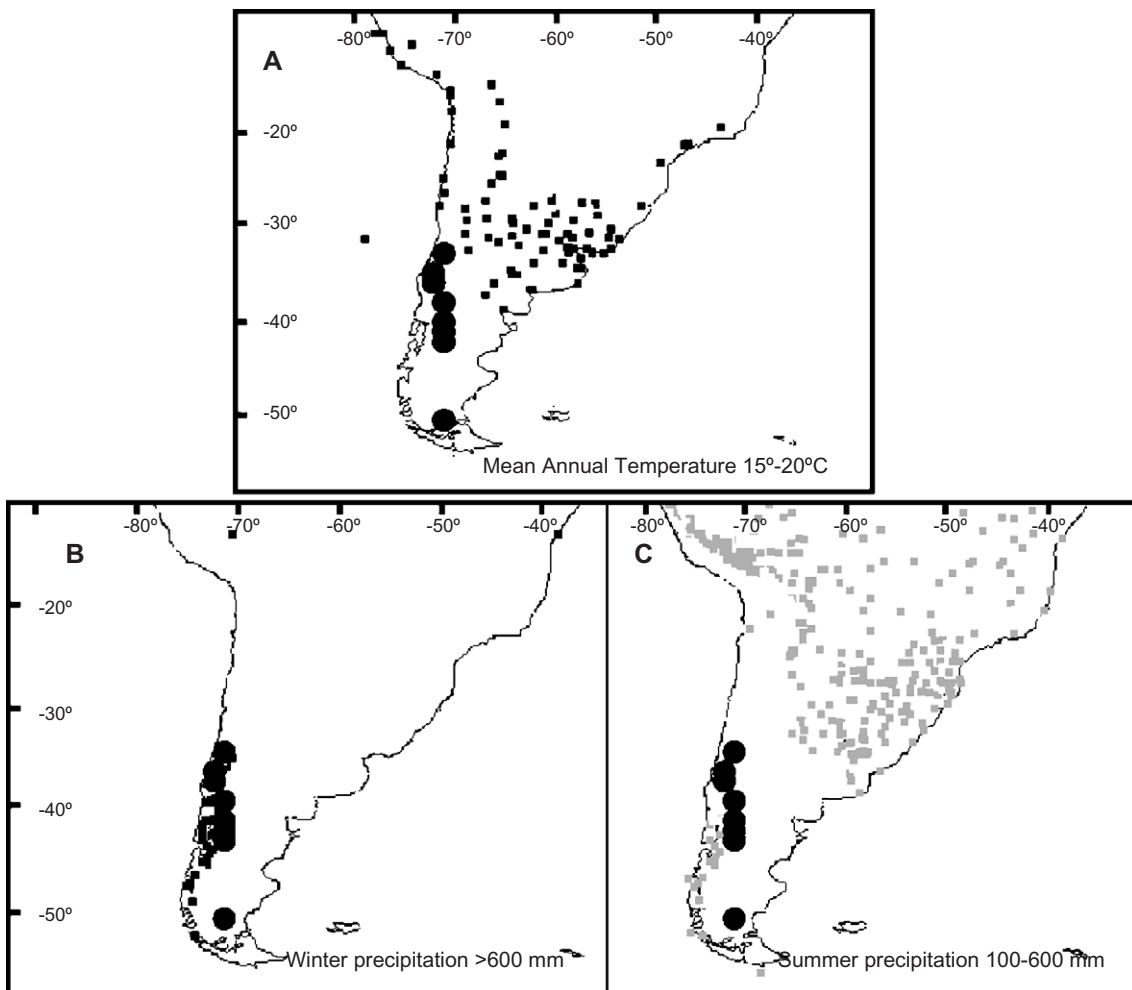


Fig. 17. Mean annual temperature between  $15$  and  $20^{\circ}\text{C}$  in southern South America (A); summer precipitation (January–March) between  $100$  and  $600\text{ mm}$  (B); and winter precipitation (July–August) upper  $600\text{ mm}$ . According to López and Aceituno (1998). Black circle: geographical position of Mixed Paleofloras.

and Cook, 1995; Sewall et al., 2000; Sloan et al., 1999).

The *Nothofagus* species recorded in these taphofloras are probably one of the best examples of adaptation to the climate scenario proposed. As shown by our results, fossil species had a broader disposition in the multivariate space of the correspondence analysis with 60% of these bearing morphologies not related with modern *Nothofagus*. Hence, these results offer insight into the broader climate envelopes present in the fossil species. Other important and very diverse families present in these Mixed fossil floras were the Lauraceae and Myrtaceae (Hinojosa and Villagrán, 1997; Troncoso and Romero, 1998), both of which have warm-humid requirements that agrees with the paleoclimate hypothesis proposed here. As an example, between 15% and 30% of the woody angiosperms from the fossil floras of the lower to middle Eocene at Pichileufú and Río Turbio (Berry, 1938; Hünicken, 1967) correspond to these families. This percentage climbs to over 48% at the Miocene localities of central Chile, Goterones and Boca Pupuya (Troncoso, 1991).

In our search for a modern analogue of the climate during the Cenozoic, we have placed the modern floras of the forests of the Pacific Coast of central–southern Chile within a region bounded by the parameters considered critical for the existence of the Mixed fossil floras: MAT and summer rains (Fig. 16). As indicated by our leaf physiognomic analyses, these floras existed within a MAT range of 15–20 °C and 200–600 mm of summer precipitation. The modern temperate rainforests of central–southern Chile receive similar precipitation amounts but are clearly adapted to colder temperatures than the Mixed fossil floras (Fig. 17). Likewise, the subtropical sclerophyllous forests of the Mediterranean region of central Chile have similar temperature requirements but receive much smaller amounts of summer precipitation (<100 mm).

The distribution of summer (January–March) rainfall between 100 and 600 mm and winter (July–August) rainfall >600 mm is indicated in Fig. 16 along with the regions where MAT is between 15 and 20 °C (López and Aceituno, 1998). Only three regions exhibit similar climate

regimes to the one exhibited by the Mixed fossil floras: the eastern slopes of Bolivia, northwest Argentina and southern Brazil. Most of the eastern slope of the Argentine Andes, however, is today winter dry and receives precipitation almost exclusively in summer.

We thus conclude that the Cenozoic Mixed Paleofloras of southern South America evolved as a response to a climate regime characterized by relatively warm temperatures and rainfall throughout the year. This was made possible by the existence of a subtropical climate that extended 40°S in latitude with moisture brought in by the tropical easterlies during the summer and by the polar westerlies during the winter. This regime with no modern analogue could only have existed with a much lower Andes Cordillera, as the present-day elevations produce a severe rainshadow on the major circulation systems of the southern cone of South America.

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#### Appendix A. Regression plots of physiognomic analysis to estimate paleoclimate in southern South America, $N=161$

Fig. A1.

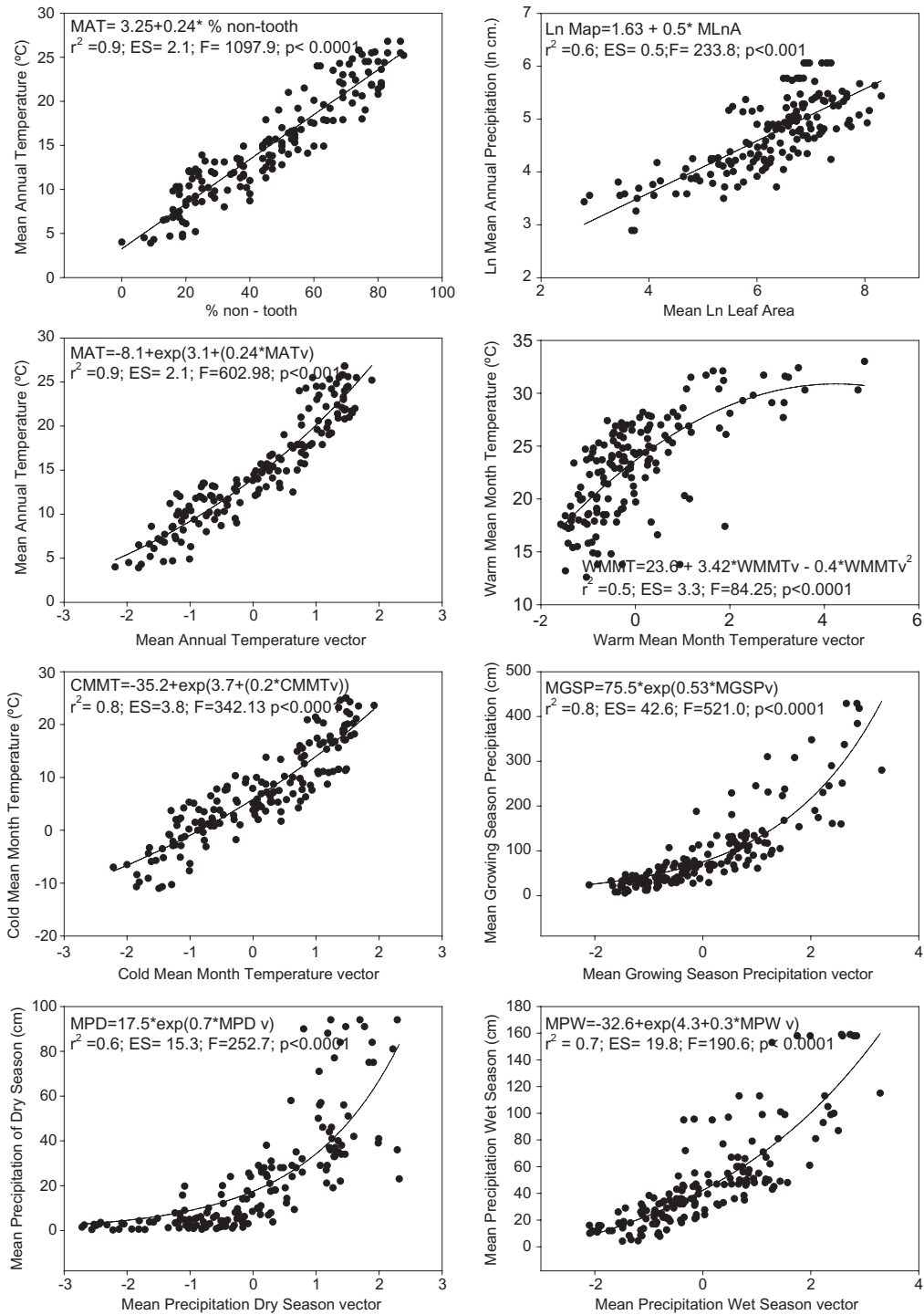


Fig. A1.

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