ORIGINAL ARTICLE

Are Chilean coastal forests pre-Pleistocene relicts? Evidence from foliar physiognomy, palaeoclimate, and phytogeography

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ABSTRACT

Aim We ask whether contemporary forests of the Chilean Coastal Range can be considered to be direct and conservative descendants of pre-Pleistocene palaeofloras that occurred in southern South America from the Palaeogene to early Neogene periods (65–10 Ma), maintaining foliar physiognomies that do not match their present-day climate. We also identify the most likely ancestors of present-day coastal forests.

Location Coastal Range of south-central Chile (33–40° S).

Methods We compared leaf morphology between five representative modern floras from mid-latitude forests of the Chilean Coastal Range, and 14 Palaeogene–early Neogene palaeofloras from southern South America. We also compared the composition of biogeographical elements (defined by the modern distribution of plant genera) between fossil and present-day assemblages. Palaeoclimatic reconstructions were based on a canonical correspondence analysis between leaf morphology of modern assemblages and eight climatic variables, and tested by a Monte Carlo permutation test. We compared the relative positions of fossil and modern floras on the environmental vector space defined by Canoco, and on axes defined by instrumental and estimated temperature and precipitation data.

Results According to foliar characters, Palaeogene palaeofloras were strikingly divergent from present-day coastal forests of central Chile. In contrast, two extant forest floras of the Chilean Coastal Range have a foliar morphology that resembles some late Eocene to early Miocene mixed palaeofloras, at least 23 Myr older. These two modern sites are representative of an area of the Coastal Range (36–37° S) that has been highlighted for its relictual character. None of the 14 fossil floras corresponded exactly to the modern composition of phytogeographic elements, although correspondence analyses showed that mixed and Neogene subtropical fossil floras were compositionally close to the extant woody floras of coastal forests in central Chile.

Main Conclusions Contemporary forests of the Chilean Coastal Range exhibit strong physiognomic resemblance to the mixed palaeofloras from 33°57′ to 41°15′ S, which may be the closest ancestor of the deciduous and endemic-rich Maulino forest, presently restricted to coastal areas between 36° and 38° S. In turn, the Neogene subtropical palaeoflora that occurred in the Proto-Andean foothills of central Chile is the likely predecessor of Mediterranean-type sclerophyllous forests of central Chile (32–33° S). Despite foliar resemblance between the late pre-Pleistocene and extant forest floras, our palaeoclimatic reconstructions suggest that modern assemblages exist under climatic conditions that do not match their foliar physiognomy. We attribute this convergence in foliar morphology to the 'evolutionary inertia' of surviving lineages, favoured by the buffering effect of the coastal environment on climatic variability.

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INTRODUCTION

Present-day rain forests of southern South America are separated from other forested regions in the continent by more than 1000 km of arid and semi-arid lands (Villagrán, 1993, 1995; Villagrán & Hinojosa, 1997). This vicariant distribution dates back to the development of hyperarid climates in the western margin of South America during the Plio-Pleistocene transition, resulting from the strong rain shadow produced by the Andean uplift (Villagrán, 1993, 1995; Villagrán & Hinojosa, 1997). Due to the prolonged geographical isolation of this region and the buffering effect of the Pacific Ocean on the temperature of the western margin of the continent, especially at mid latitudes in the Chilean Coastal Range (35–42° S), this region has been postulated as an important refuge for the biota during the Pleistocene glaciations (Villagrán, 1995, 2001).

Geological and palynological studies have shown that coastal forests were little affected by the ice ages of the Quaternary, which strongly impacted the Andes and southern Patagonia (Villagrán et al., 1995; Villagrán & Hinojosa, 1997; Villagrán & Armesto, 2005). The geographical distribution of forest taxa indicated that Chilean forests have conserved their ancient historical links with widely disjunct floras. Many plant genera

from the Chilean forests currently exhibit notable disjunctions with distant regions of the globe, such as Australasia (7.3% of the genera), New Guinea, New Zealand and East Australia (12.7%), and the South American tropics (16.7%), in addition to having a high proportion (nearly 32%) of endemic genera (Arroyo et al., 1995; Villagrán & Hinojosa, 1997). This blend of phytogeographic elements that characterizes contemporary forests of south-central Chile can be traced back to the ancient palaeofloras that occupied southern South America during the Palaeogene and early Neogene periods, under markedly different climatic and geological settings (Schmithüsen, 1956; Hinojosa & Villagrán, 1997; Villagrán & Hinojosa, 1997; Hinojosa, 2003, 2005).

Several models (Romero, 1978, 1986; Hinojosa & Villagrán, 1997; Troncoso & Romero, 1998) have proposed a succession of palaeofloras in southern South America during the Palaeogene–early Neogene periods. After examining 14 fossil floras from this period, Hinojosa (2003, 2005) postulated a series of four distinct palaeofloras (Fig. 1). A Gondwanic tropical palaeoflora developed during the Palaeocene in a southern territory region that was still continuous with western Antarctica and Australia. From the beginning of the Eocene, this tropical palaeoflora was replaced by a Gondwanic subtropical palaeoflora, under cooler conditions, presumably
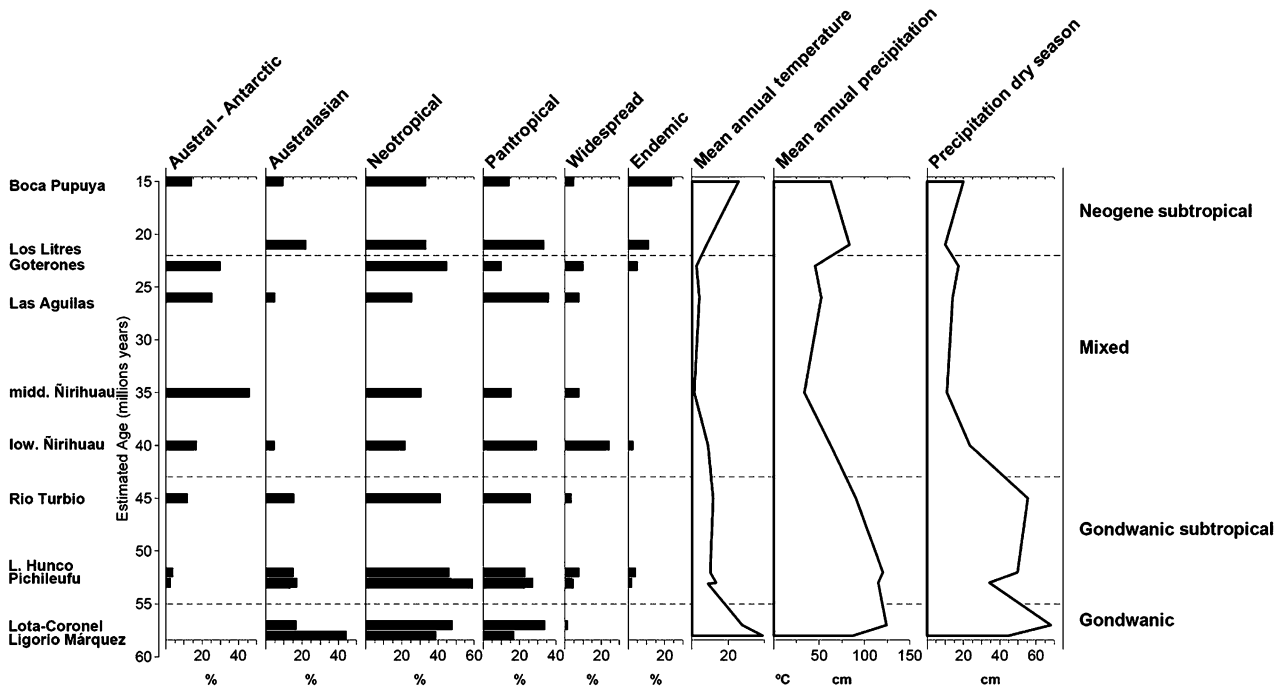

Figure 1 Phytogeographic spectra and palaeoclimatic reconstruction for pre-Pleistocene fossil floras from southern South America. Broken lines define different palaeofloras and their associated palaeoclimate (modified from Hinojosa, 2005).

with a bi-seasonal precipitation regime (Hinojosa & Villagrán, 2005; Hinojosa, 2005). From the end of the Eocene until the beginning of the Miocene, a mixed palaeoflora developed in southern South America under a cooler and less humid climate, associated with the onset of the Antarctic glaciation (Hinojosa & Villagrán, 1997). Throughout the Miocene, under relatively warmer and wetter climate than in the preceding period, a Neogene subtropical palaeoflora occupied central Chile, coinciding with a global warm event ($\Delta T = 6$–$9\ ^{\circ}C$) (Fig. 1). Concomitantly, the Andean rainshadow effect became significant during this period (Gregory-Wodzicki, 2000b), presumably reducing or stopping the flow of humid air from the east.

The geographical isolation of forests in southern South America dates back several million years from the Plio-Pleistocene boundary. Due to the limited impact that glacial events had on Chilean coastal forests, we expect that these ecosystems will show important legacies of the palaeofloras that successively occupied southern South America during the Palaeogene–early Neogene periods. In this study, we ask whether contemporary forests of the Chilean Coastal Range

can be considered direct and conservative descendants of these palaeofloras, exhibiting physiognomic traits that are in agreement with pre-Pleistocene palaeoclimates. We also identify the most likely ancestors of the present-day forests. Our analysis is based on a comparison of leaf morphology and climatic indices between five representative modern floras (Table 1) from the mid-latitude forests of the Chilean Coastal Range (33–40° S) and 14 Palaeogene–early Neogene palaeofloras from southern South America (Fig. 1, Table 2). We reconstructed the palaeoclimates under which these ancient floras developed and compared them with the climatic data for modern floras. Finally, we also compared the composition of biogeographical elements (defined by the modern distribution of plant genera) between fossil and present-day assemblages.

METHODS

Analysis of leaf morphology

Sampling of modern foliar material was conducted in five regionally representative native forests of the Coastal Range of

Table 1 Coastal Range sites (33 and 40° S) and present-day forests considered in this study, including their latitudinal location, altitudinal range, aspects, and number of leaf samples collected. FT, forest type; L, latitude (° S); AR, altitudinal range (m); SA, slope aspect; B/LS, no. of branches/no. of leaves sampled

Locality	FT	L (° S)	AR	SA	B/LS
L. Campana	Sclerophyllous	33°	400–800	East	261/2610
L. Ruiles	Deciduous 'Maulino'	35°50′	200–400	East	213/2451
L. Queules	Deciduous 'Maulino'	35°59′	400–500	East	292/3242
Nahuelbuta	Mixed deciduous-evergreen	37°49′	400–800	East	186/1971
C. Pelada	Broad-leaved evergreen	40°13′	0–400	West	216/1481

Table 2 Fossil floras considered for foliar morphology and phytogeographic analyses. Sources: 1, literature; 2, collection, Lab. Ecología y Sistemática Vegetal, Universidad de Chile; 3, collection, Museo de Historia Natural, Santiago, Chile; 4, collection, Museo Argentino de Historia Natural, Buenos Aires, Argentina; 5, collection, Lab. Palaeobotánica Universidad de Buenos Aires, Argentina; 6, collection, Museo Palaeontológico, Universidad de Concepción, Chile. Geographic location, phytogeographic character, absolute and/or relative age (when available), and number of taxa analysed per flora are shown

Fossil floras	Geologic age	Dates (Ma)	Latitude (° S)	Phytogeographic character	No. taxa	Collections
Jakokkota*	Upper Miocene	10.6 (Ar/Ar)	17°17′	Subtropical	31	2
Potosí*	Lower–Middle Miocene	20–13 (Ar/Ar)	19°61′	Subtropical	35	1
Boca Pupuya	Middle–Upper Miocene	?	33°57′	Subtropical	27	3
Los Litres	Lower Miocene	21 (Ar/Ar)	33°18′	Subtropical	20	2
Goterones	Lower Miocene	23 (Sr)	33°57′	Mixed	28	3
C° L. Aguilas	Upper Oligocene	26–23 (Ar/Ar)	33°19′	Mixed	42	2
Midd Ñirihuau	Oligocene	?	41°19′	Mixed	18	1
Low Ñirihuau	Eocene–Oligocene	?	41°15′	Mixed	33	1
Rio Turbio	Middle Eocene	?	51°33′	Subtropical Gondwanic	72	1
L. Hunco	Lower Eocene	52 (Ar/Ar)	42°27′	Subtropical Gondwanic	30	1,4,5
Pichileufu	Lower Eocene	?	41°7′	Subtropical Gondwanic	120	1,5
Cocholgüe*	Palaeocene–Eocene	?	36°35′	Gondwanic	30	6
Lota-Coronel	Upper Palaeocene	?	37°	Gondwanic	94	1
L. Marquez	Upper Palaeocene	< 57 (K/Ar)	46°45′	Gondwanic	19	1

*Floras that were not included in the phytogeographic analysis.

south-central Chile, between 33 and 40° S (Table 1).Villagrán (2001) suggested that this area was the most important refuge for the biota during the Pleistocene glaciations. In each forest site, fresh samples of leaves from at least 30 dicotyledonous woody species (trees, shrubs and vines) were collected, across a 100-m elevation gradient. Leaf samples were digitalized (at least three samples of both sun and shade leaves per species, for a total of 11,755 leaves from all five sites) and 31 foliar characters, as defined by Wolfe (1993), were measured. Morphological characters of fossil leaves were measured for all morpho-species identified from each of the 14 sites (17–51° S, Table 2) in southern South America, following the same protocol as for modern leaves. These characters were used to characterize the foliar physiognomy of modern and fossil assemblages and for palaeoclimatic reconstructions (see Table S1 in Supplementary Material).

Palaeoclimate model

Palaeogene–early Neogene climates were reconstructed on the basis of the statistical relationships between foliar-physiognomy and modern climate (Sinnott & Bailey, 1915; Bailey & Sinnot, 1916; Dilcher, 1973; Dolph & Dilcher, 1979; Wolfe, 1979; Kovach & Spicer, 1996). The relationships between 31 foliar traits of modern dicotyledonous assemblages and their respective climatic variables were assessed (Wiemann *et al.*, 1998; Gregory-Wodzicki, 2000a; Hinojosa & Villagrán, 2005; Hinojosa, 2005). To build the climate model we used a modified database containing both climatic and leaf character information from 140 localities from North America, Asia and South America (Wolfe, 1993; Gregory-Wodzicki, 2000a), adding the data for Chilean forests sampled in this study (CLAMP3B SA database). A canonical correspondence analysis (CCA; CANOCO version 4 for Windows, Microcomputer Power, Ithaca, NY, USA) was used to explore the relationship between leaf morphology of modern assemblages and eight climatic variables (Table 3). Foliar traits of the 14 fossil floras (Table 2) were added to this database as passive samples.

The statistical significance of the relationships between leaf traits and climatic variables was assessed using a Monte Carlo permutation test (Manly, 1991). This statistical test was based on 1000 permutations of the data matrix of leaf characters and climatic variables per site (ter Braak & Smilauer, 1998). To infer palaeoclimates, the relative positions of each fossil and modern flora on the environmental vector space defined by CANOCO were compared graphically.

Phytogeographic elements

All taxa in fossil and modern floras were assigned to six phytogeographic elements defined by the modern distributions of the woody genera according to Willis (1985), Mabberley (1987), Villagrán & Hinojosa (1997) and Gayó (2004). Assignment of fossil taxa to phytogeographic elements was based on the current knowledge of South American fossil genera in the palaeobotanic literature (see Villagrán & Hinojosa, 1997 and references therein). Elements were defined as follows.

(1) Austral-Antarctic – temperate elements (AA); genera with disjunct distributions at mid and high latitudes of the southern hemisphere, including New Zealand, Tasmania, SE and Southern Australia, and southern South America (e.g. *Eucryphia*, *Laurelia*).

(2) Australasian tropical elements (AU); genera distributed in southern hemisphere territories, occasionally extending their range into tropical and subtropical regions of NE Australia, New Guinea, Malaysia, Indomalaysia, SE Asia and the western Pacific islands (e.g. *Drimys*, *Griselinia*). Some of these genera also occur in tropical regions of the Americas.

(3) Neotropical elements (N); genera with disjunct distributions in southern South American forests and montane forests of the eastern Andes (NW Argentina, Bolivia and Peru) and/or the Atlantic coast of southern Brazil, sometimes extending to Central America (e.g. *Azara*, *Myrceugenia*).

(4) Pantropical elements (P); genera occurring in the circumtropical belt, incorporating South America, Indo-Malaysia, Africa and Madagascar (e.g. *Prosopis*, *Cryptocarya*). Some of these genera are absent from tropical Australasia.

(5) Widespread elements (W); genera with world-wide distributions, including tropical, subtropical and temperate regions (e.g. *Senecio*, *Berberis*).

(6) Endemic elements (E); genera presently restricted to Chilean subtropical and temperate forests, south of 30° S. However some of these also occur along the western margin of

Table 3 Environmental variables used in the canonical correspondence (top eight) and the linear regression (mean annual precipitation) analyses. For the Chilean Coastal Range sites, we used data from the nearest meteorological station (Di Castri & Hajek, 1976)

Locality	MAT	WMMT	CMMT	LGS	MPGS	MMPGS	3-WET	3-DRY	Station
L. Campana	14.4	19.1	10.0	12.0	50.1	4.2	32.8	1.4	Quilpue
L. Ruiles	15.3	22.0	8.7	9.0	28.9	3.2	39.5	3.0	Cauquenes
L. Queules	15.3	22.0	8.7	9.0	28.9	3.2	39.5	3.0	Cauquenes
Nahuelbuta	12.8	19.0	7.9	9.0	27.6	3.5	55.2	6.2	Angol
C. Pelada	11.3	13.8	9.0	8.0	104.9	13.1	95.5	25.6	Pta. Galera

MAT: mean annual temperature (°C); WMMT: warmest month mean temperature (°C); CMMT: coldest-month mean temperature (°C); LGS: length of growing season (number of months with temperature higher than 10 °C); MPGS: mean precipitation during the growing season (cm); MMGS: mean-monthly precipitation during growing season (cm); 3-WET: precipitation of three consecutive wettest months (cm, wet season); 3DRY: precipitation of three consecutive driest months (cm, dry season).

the Andes in Argentina, south of 37° S (e.g. *Peumus*, *Luma*, *Aextoxicon*). To determine the similarities in composition of phytogeographic elements among current and fossil floras, we conducted a correspondence analysis (CANOCO version 4 for Windows, 1998).

RESULTS

Foliar morphology and palaeoclimatic reconstruction

For the data set examined, the first two canonical axes (Fig. 2) explained 87.7% of the total variance in the leaf morphology and climatic variables. Modern foliar morphology was found to be strongly associated with environmental variables (CLAMP 3B SA axes; F-ratio = 31, 5; $P < 0.001$, Monte Carlo test), supporting the use of this model for the reconstruction of pre-Pleistocene climates. Axes 1 and 2 discriminated climatic differences in temperature and precipitation, respectively.

All five modern coastal forests were clearly segregated in the canonical vector space from Palaeogene fossil floras (Gondwanic tropical palaeoflora and Gondwanic subtropical palaeoflora). According to the model, Palaeogene fossil floras have a distinct foliar physiognomy and occurred under a much warmer and more humid climate (Fig. 2) than present-day forests. In the same way, the Neogene subtropical palaeoflora developed under a palaeoclimate distinct from present-day forests (Fig. 2). Pre-Pleistocene palaeofloras that would have resembled the foliar physiognomy and therefore the climatic
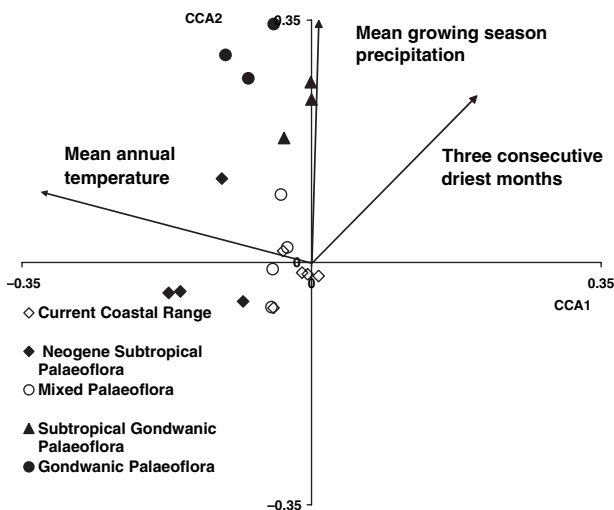

Figure 2 Bi-plot of canonical correspondence analysis based on CLAMP 3B SA database ($n = 161$ data points). The first two canonical axes explain 87.7% of the total variance. Axis one (CCA1) discriminates sites based on differences in temperature, while axis two (CCA2) does it on the basis of precipitation differences. Bi-plot shows the mean annual temperature vector ($r = -0.88$ with CCA1); mean growing season precipitation vector ($r = 0.84$ with CCA2); and dry season precipitation vector ($r = 0.58$ with CCA2). The relative positions of fossil floras and present-day coastal floras of southern South America are shown by the symbols.

condition found in modern forests are the mixed palaeofloras from the end of the Eocene (Fig. 2).

Modern floras of the Chilean Coastal Range were distributed along the *x*-axes of Fig. 3 according to their latitudinal location, from the northern warmer sites (La Campana and Los Queules, Table 1), to the southern temperate sites (Pelada Mountain range, Table 1). The distribution of the main South American palaeofloras, along the *x*-axes of Fig. 3, was coupled to their age from the Palaeogene (right) to the Neogene (left). According to the mean annual temperature vector of the CCA, the Palaeogene Gondwanic palaeoflora was an average of 10 °C warmer than any present day site (Fig. 3a,d), however, the late Eocene mixed palaeofloras occurred under temperature conditions that resembled the conditions of contemporary deciduous forests from Los Ruiles and Los Queules (Fig. 3a). The Neogene subtropical palaeoflora, on the other hand, departs from the tendency of declining mean annual temperatures, recorded globally since the Palaeogene (Zachos *et al.*, 2001; Hinojosa & Villagrán, 2005; Hinojosa, 2005), returning to the warm conditions of the ancient Gondwanic tropical palaeoflora (Fig. 3d). Regarding the position of modern and fossil floras on the CCA precipitation (MPGS) vector, some present-day floras are undistinguishable from both Neogene subtropical and mixed palaeofloras (Fig. 3b). In contrast, the Gondwanic tropical palaeoflora stands out, with an estimated palaeo-precipitation well above any contemporary site (Fig. 3b,e). According to the precipitation during the dry-season vector (3Dry), lower latitude floras from the Chilean Coastal Range matched the conditions of the Eocene/Oligocene – lower Miocene mixed palaeofloras (Fig. 3c). Gondwanic tropical palaeofloras from the Palaeogene occupied the wettest position along this vector (Fig. 3c). In contrast, the Neogene subtropical fossil floras from Bolivia and Cerro Los Litres (Chile) fall in the driest positions along the 3Dry vector (with one exception, Boca Pupuya).

Despite the similarity in temperature and precipitation conditions between modern coastal forests and the late Eocene to early Miocene floras, derived from the leaf physiognomy analysis (Fig. 3a–c), temperature data for the two southernmost modern sites fall below the estimates for their closest fossil relatives (Fig. 3d). In contrast, temperature estimates for the fossil sites of Goterones, Las Aguilas and Nirihuau roughly match the climatic data for the remaining three northern sites. Regarding precipitation, all the modern localities, except for C. Pelada (the southernmost site) are drier than any estimate for the fossil sites (Fig. 3e–f).

Phytogeographic spectra of modern and fossil floras

The extant flora of the northernmost forest site (La Campana) in central Chile is co-dominated by Neotropical (27%), Widespread (24%) and Endemic (22%) elements (Fig. 4a). Australasian and Pantropical genera accounted for only 14% each, while Austral-Antarctic elements are absent. Modern deciduous forests at the Los Ruiles site (35°50′ S) are also dominated by Neotropical (32%) and Endemic (24%) ele-
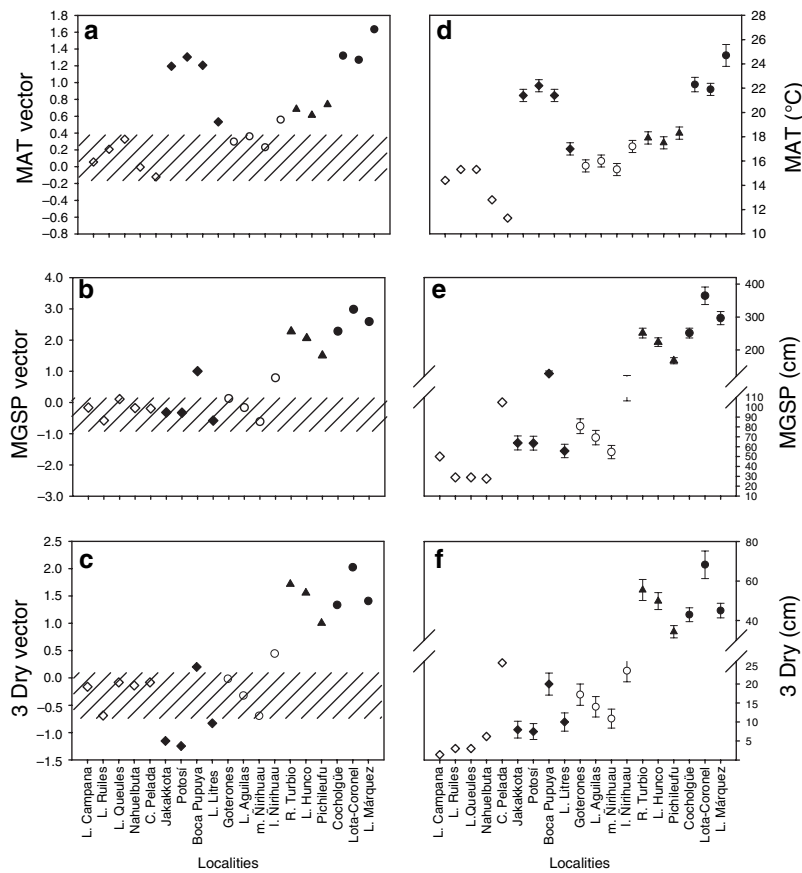
Figure 3 Distribution of the present-day Coastal Range forest sites and Palaeogene–early Neogene fossil floras on vectors based on leaf physiognomic CCA (Fig. 2). (a) Mean annual temperature (MAT) vector. (b) Mean growing season precipitation (MGSP) vector. (c) Dry season vector (three consecutive driest months, 3DRY). The shaded area represents the range of the data for modern Coastal Range forests. (d–f) Estimated values and instrumental climatic data for fossil and modern floras. Bars are 95% confidence intervals. Open diamonds: modern Coastal Range forests. Black diamonds: Neogene subtropical palaeofloras. Open circles: mixed palaeofloras. Black triangles: Gondwanic subtropical palaeofloras. Black circles: Gondwanic tropical palaeofloras.

ments, but Austral-Antarctic genera increase to 19% (Fig. 4b). In the geographically nearby site of Los Queules (35°59′ S), Endemic genera (36%) become dominant, followed by a balanced distribution of the remaining elements, except for poorly represented Widespread genera (Fig. 4c). Modern forests of the Nahuelbuta Range (37°49′ S) have a high proportion of Austral-Antarctic (23%) and Australasian (20%) elements, followed by Pantropical (17%) and Widespread genera (17%) (Fig. 4d). Endemic (13%) and Neotropical (10%) elements tend to decline. Finally, in the southernmost site, Cordillera Pelada (40° S), Endemic elements increase again (38%), followed by Australasian and Neotropical elements (19% and 17% respectively) (Fig. 4e). Austral-Antarctic and Widespread elements add up to 12%, while the Pantropical genera are nearly absent.

The composition of most fossil floras shows the strong dominance of Neotropical elements. The oldest floras (Ligorio Márquez; Lota – Coronel from the Palaeogene) were dominated by genera that are represented today in all the warmest regions of the planet, including Australasian, Neotropical and Pantropical genera. Eocene palaeofloras, in turn, are dominated by elements that are presently Neotropical and Pantropical in distribution, with a lower proportion of Australasian and a very small presence of Austral-Antarctic elements. During the subsequent lapse from the upper Eocene to lower Miocene, fossil floras exhibited a more balanced blend of elements of various

biogeographical origins. Finally, in the remainder of the Miocene, fossil floras were again dominated by Neotropical, Pantropical and Australasian elements, with a decline of Austral-Antarctic elements. For the first time in this period, we note a significant presence of genera that are presently endemic to the southern forests.

These shifting biogeographical compositions are associated with the succession of the Gondwanic tropical and subtropical; mixed and Neogene subtropical palaeofloras as described by Hinojosa (2003, 2005). The first two axes of the correspondence analysis (Fig. 5), based on the composition of biogeographical elements in fossil and modern floras, explained 76.8% of the total variance. The placement of each flora along the first axis represents the relative importance of endemics (70% of axis 1 variance), Neotropical (60%) and Pantropical (54%) elements. In turn, axis 2 reflects floristic dominance by Austral-Antarctic (69%) and Australasian elements (55% of axis 2 variance). In this representation, the present-day floras of central Chile (Fig. 5) resemble the Neogene subtropical flora of Boca Pupuya and the mixed palaeofloras due to their similar representation of Endemic and Austral-Antarctic elements. A second correspondence analysis was performed to correct for the strong influence of Endemic elements on the results of the first analysis, as this element is poorly represented for most palaeofloras in southern South America. In both correspondence analyses the oldest palaeofloras (Gondwanic tropical and subtropical) were clearly distinct in their element composition
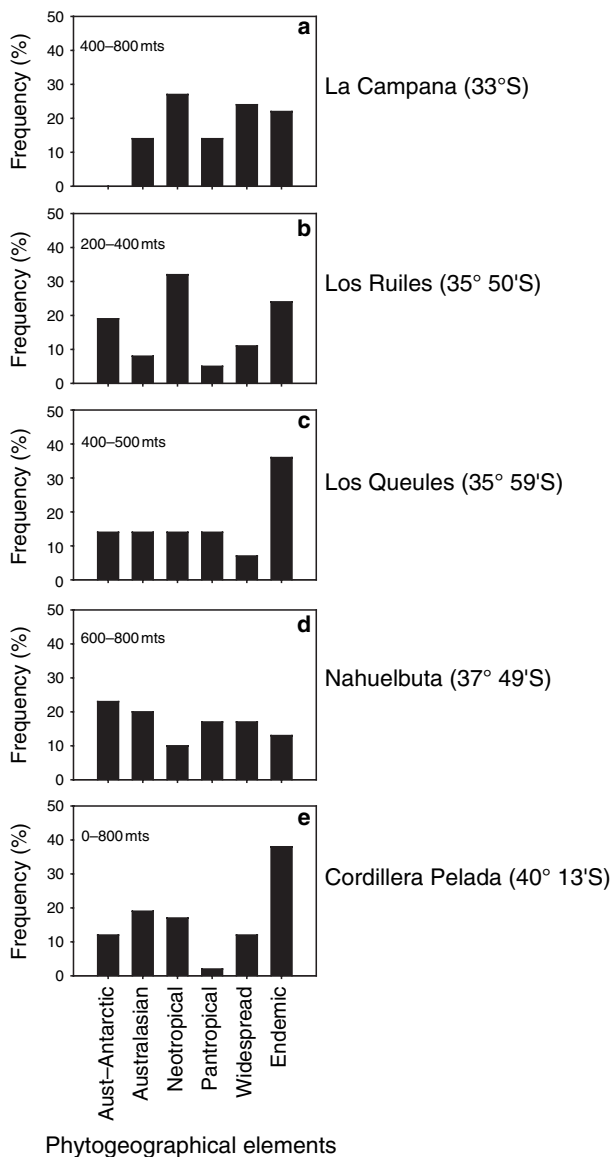
Figure 4 Phytogeographic spectra of extant forests from the Chilean Coastal Range, arranged (top to bottom) from mediterranean to temperate latitudes (33–40° S). See text for definition of phytogeographic elements.

from the mixed palaeoflora and from present-day coastal forests.

DISCUSSION

According to their foliar characters, Palaeogene palaeofloras were clearly divergent from present-day coastal forests of central Chile. Substantial morphological differences reflect that the prevailing palaeoclimate during the early Cenozoic has no modern analogue at mid latitudes in southern South America (Hinojosa & Villagrán, 1997, 2005; Hinojosa, 2003, 2005). In contrast, extant forest floras of the Chilean Coastal Range (Los Ruiles and Los Queules, 36° S) have a foliar morphology that

notably resembles some Oligocene to early Miocene mixed palaeofloras (Goterones, middle Ñirihuau and Cerro Las Aguilas), at least 23 Myr older. These two modern sites are representative of an area of the Coastal Range (36–37° S) that has been highlighted for its relictual character (Villagrán *et al.*, 1998).

Extant floras at this latitude have a high proportion of woody species (> 50% of the total flora, Arroyo *et al.*, 1995) and a high concentration of narrow endemics, including *Pitavia punctata*, *Nothofagus alessandrii*, *N. glauca*, and *Gomortega keule*; the latter is the only member of the endemic family Gomortegaceae (Marticorena & Rodriguez, 2001).

Nothofagus alessandrii, a narrow endemic, which is restricted to these coastal forests, is considered the most primitive living species in the genus (Melville, 1973; Humphries, 1981; Tanai, 1986; Gandolfo, 1994; Manos, 1997). Despite foliar resemblance between the mixed palaeofloras of the Oligocene-early Miocene (Goterones, middle Ñirihuau and Cerro Las Aguilas) and extant forest floras from mid-latitudes in the Chilean Coastal Range (Fig. 3a–c), our palaeotemperature and palaeoprecipitation reconstructions suggest that modern assemblages exist under climatic conditions that do not match their foliar physiognomy (Fig. 3d–f). Consequently, we attribute their convergence in foliar morphology of woody species with the mixed palaeofloras to the 'evolutionary inertia' of the surviving lineages, favoured by the buffering effect of the coastal environment on climatic variability. Foliar characters of modern lineages, therefore, tend to overestimate current precipitation in the area of the Maulino forest (Fig. 3e,f). This applies particularly to the northern localities (33–36° S) in the Chilean Coastal Range, which at present are subjected to pronounced summer droughts, characteristic of the modern Mediterranean climate (Van Husen, 1967; Miller, 1976) developed at least since the late Miocene. Our analysis suggests that the ancestors of modern floras evolved under a much wetter climate, and consequently should be undergoing range contraction towards wetter and less variable sites at coastal areas. This range contraction has presumably been constrained, especially during glacial periods, by lower temperatures at higher latitudes along the western margin of South America.

Palaeobiogeography

The modern spectra of phytogeographic elements of coastal forest sites at mid latitudes resembles the overall pattern described for Chilean forests by Villagrán & Hinojosa (1997). None of the 14 fossil floras corresponded exactly with the modern composition of phytogeographic elements (Figs 1 & 4), although interesting convergences exist. For example, both correspondence analyses showed that mixed and Neogene subtropical fossils floras (i.e., Boca Pupuya) were compositionally similar to the extant woody floras of coastal forests in central Chile (Fig. 5). The modern flora of Cerro La Campana (32° S) in the central Chilean Coastal Range and the Neogene
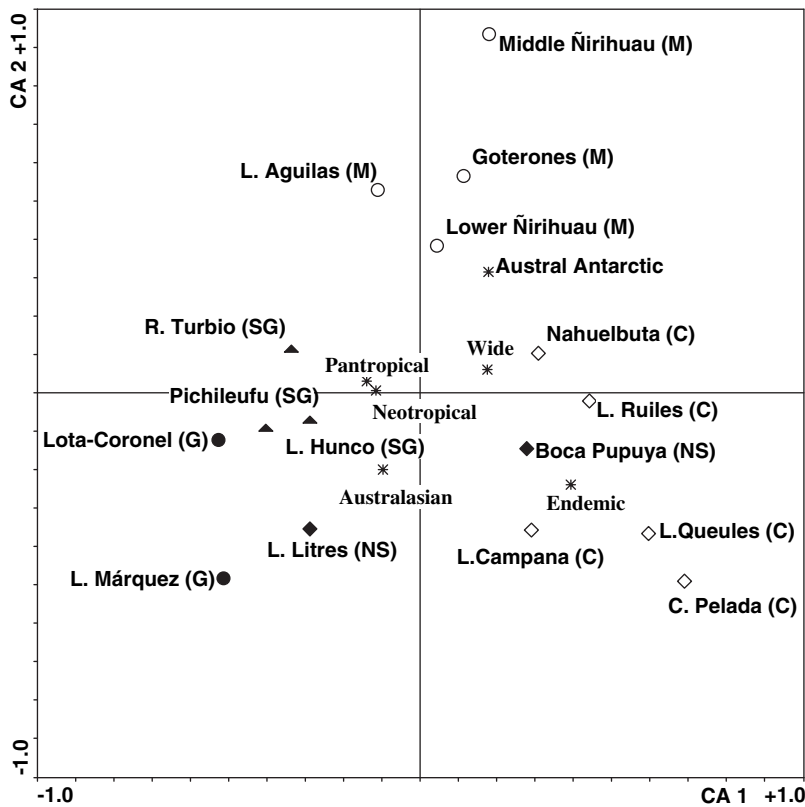
Figure 5 Correspondence analysis comparing phytogeographic spectra (stars) of modern and fossil floras from southern South America. The positions of modern Coastal Range floras in south-central Chile and pre-Pleistocene fossil floras included in this study are shown by the symbols. The first two CA axes explain 76.8% of the total variance. C, current floras; NS, Neogene subtropical palaeofloras; M, mixed palaeofloras; SG, Gondwanic subtropical palaeofloras; G, Gondwanic tropical palaeofloras (Table 2).

subtropical fossil flora of Cerro Los Litres (Miocene, central Chile, 33° S) are dominated by Neotropical and Endemic elements, and are characterized by an absence of Austral-Antarctic elements.

The correspondence analysis places Cerro La Campana close to another Neogene subtropical flora, Boca Pupuya (Fig. 5). The presence in the Miocene fossil flora of Cerro Los Litres (Table 2) of contemporary sclerophyllous genera, such as *Persea, Peumus, Beilschmiedia* and *Cryptocarya*, which are found today in Cerro La Campana, on the Chilean Coastal Range, suggests that this palaeoflora may be the nearest predecessor of the modern subtropical mediterranean forests of central Chile (Hinojosa, 1996; Hinojosa & Villagrán, 1997; Selles & Hinojosa, 1997; Villagrán &Hinojosa, 1997). However, the palaeoclimate that characterized palaeofloras such as Cerro Los Litres, from 20 Ma, differed substantially from the modern climate of central Chile. Palaeoclimatic reconstruction, based on CCA vectors (Fig. 3), suggests a much warmer climate. The age of this palaeoflora coincides with the beginning of a Mid-Miocene global warming period, identified by Zachos *et al.* (2001), based on sea surface temperatures. In addition, geological evidence indicates that Miocene precipitation was still weakly affected by the rain shadow effect of the uplifting Andes (Hinojosa, 1996, 2003, 2005; Hinojosa & Villagrán, 1997, 2005; Villagrán & Hinojosa, 1997; Gregory-Wodzicki, 2000b). Consequently, it is unlikely that this vegetation faced the pronounced summer droughts that characterize central Chile today.

We show here that the mixed palaeofloras of Cerro Las Aguilas and Goterones (upper Oligocene and early Miocene, Table 1) in central Chile (Troncoso, 1991; Hinojosa, 1996; Selles & Hinojosa, 1997) are similar in foliar physiognomy to the modern floras of Los Queules and Nahuelbuta (36–38° S) in the Chilean coastal range.

CONCLUSION

In conclusion, our results suggest that some late pre-Pleistocene palaeofloras, particularly the mixed and Neogene subtropical palaeofloras, may be the nearest predecessors of contemporary, mid-latitude forests of the Chilean Coastal Range. Based on the composition of genera, phytogeographic spectra and foliar physiognomies, the mixed palaeoflora which developed in central Chile during the Oligocene–Miocene transition, *c.* 25 Ma, is closely related to the extant deciduous Maulino forest, represented in Los Ruiles and Los Queules (36° S, Table 1). The subsequent Neogene subtropical palaeoflora that occupied central Chile during the lower to mid Miocene, 20–15 Ma, and which developed under a warmer and more humid palaeoclimate, with an incipient Andean rain shadow effect (Hinojosa, 1996, 2003, 2005; Hinojosa & Villagrán, 1997, 2005; Villagrán & Hinojosa, 1997; Gregory-Wodzicki, 2000b), is the nearest ancestor of the sclerophyllous vegetation of central Chile. These pre-Pleistocene palaeofloras presumably configured the contemporary floristic assemblages represented today in coastal forests of south-central Chile

(32–33° S) and their closest descendants have survived in the unglaciated, mid latitude coastal range.

The convergent phytogeographic spectra and foliar physiognomy of fossil and present-day floras, and the floristic singularity of contemporary forests in south-central Chile (36–37° S), support the idea that coastal forests are extremely conservative. The similarity between the contemporary forests and late pre-Pleistocene palaeofloras indicates notable evolutionary stability of surviving lineages, presumably including the conservation of ancient biological interactions, such as the marsupial dispersal of mistletoe seeds in the Loranthaceae (Amico & Aizen, 2000). The botanical and ecological legacies preserved in Chilean coastal forests are still evident despite massive tectonic processes and active volcanism associated with Andean uplift, and major climatic changes derived from continental glaciations characterizing the end of the pre-Pleistocene and the entire Quaternary in southern South America (Villagrán et al., 1998; Villagrán, 2001; Villagrán & Armesto, 2005). Apparently, the western margin of the continent at mid latitudes remained fairly stable through these great convulsions, allowing for the conservation of ancient floristic assemblages.

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REFERENCES

Amico, G. & Aizen, M. (2000) Mistletoe seed dispersal by a marsupial. *Nature*, **408**, 929–930.

Arroyo, M., Cavieres, L.A., Peñaloza, A., Riveros, M. & Faggi, A.M. (1995) Relaciones fitogeográficas y patrones regionales de riqueza de especies en la flora del bosque lluvioso templado de Sudamérica. *Ecología de los bosques nativos de Chile* (ed. by J.J. Armesto, C. Villagrán and M.T.K. Arroyo), pp. 71–99. Comité de publicaciones científicas, Vicerrectoría Académica, Universidad de Chile. Editorial Universitaria, Santiago.

Bailey, I.W. & Sinnot, E.W. (1916) The climatic distribution of certain types of angiosperm leaves. *American Journal of Botany*, **3**, 24–39.

ter Braak, C. & Smilauer, P. (1998) *Canoco reference manual and user's guide to Canoco for Windows: software for canonical community ordination (version 4)*. Microcomputer Power, Ithaca, NY, USA.

Di Castri, F. & Hajek, E. (1976) *Bioclimatología de Chile*. Editorial de la Universidad Católica de Chile, Santiago.

Dilcher, D.L. (1973) A paleoclimatic interpretation of the Eocene floras of southeastern North America. *Vegetation and vegetational history of northern Latin America* (ed. by A. Graham), pp. 39–59. Elsevier Scientific Publishing Company, Amsterdam.

Dolph, G.E. & Dilcher, D.L. (1979) Foliar physiognomy as an aid in determining paleoclimate. *Palaeontographica*, **170**, 151–172.

Gandolfo, M.A. (1994) Evolución del género *Nothofagus* Blume basada en su morfología foliar comparada. PhD Dissertation, Universidad de Buenos Aires, Buenos Aires, pp. 159.

Gayó, E. (2004) *Estudio taxonómico y fisionómico-climático de la tafoflora Caleta Cocholgüe (36° 35′ S y 72°58′ W), Eoceno inferior, Chile Central*. Tesis Magister Facultad de Ciencias, Universidad de Chile, Santiago, Chile.

Gregory-Wodzicki, K.M. (2000a) Relationships between leaf morphology and climate, Bolivia: implications for estimating paleoclimate from fossil floras. *Paleobiology*, **26**, 668–688.

Gregory-Wodzicki, K.M. (2000b) Uplift history of the central and northern Andes: a review. *Geological Society of America Bulletin*, **112**, 1091–1105.

Hinojosa, L.F. (1996) Estudio paleobotánico de dos tafofloras terciarias en la precordillera de Santiago de Chile Central (La Dehesa) e inferencias sobre la vegetación y el clima Terciario de Austrosudamérica. Master Thesis, Facultad de Ciencias, Universidad de Chile, Santiago.

Hinojosa, L.F. (2003) Fisionomía foliar y clima de las paleofloras mixtas del Terciario de Sudamérica. PhD Dissertation, Facultad de Ciencias, Universidad de Chile, Santiago.

Hinojosa, L.F. (2005) Cambios climáticos y vegetacionales inferidos a partir de paleofloras Cenozoicas del sur de Sudamérica. *Revista Geológica de Chile*, **32**, 95–115.

Hinojosa, L.F. & Villagrán, C. (1997) Historia de los bosques del sur de Sudamérica, I: Antecedentes paleobotánicos, geológicos y climáticos del Terciario del cono sur de América. *Revista Chilena de Historia Natural*, **70**, 225–239.

Hinojosa, L.F. & Villagrán, C. (2005) Did South American mixed paleofloras evolve under thermal equability or in the absence of an effective Andean barrier during the Cenozoic? *Palaeogeography, Palaeoclimatology, Palaeoecology*, **217**, 1–23.

Humphries, T.M. (1981) Biogeographical methods and the southern Beeches (Fagaceae: *Nothofagus*). *Advances in cladistics* (ed. by V.A. Funks and D.R. Brooks), pp. 177–207. New York Botanical Garden, New York.

Kovach, W.L. & Spicer, R.A. (1996) Canonical correspondence analysis of leaf physiognomy: a contribution to the development of a new palaeoclimatological tool. *Paleoclimates*, **2**, 125–138.

Mabberley, D.J. (1987) *The plant book. A dictionary of higher plants*. Cambridge University Press, Cambridge.

Manly, B.F. (1991) *Randomization and Monte Carlo methods in biology*. Chapman & Hall, London.

Manos, P. (1997) Systematics of *Nothofagus* (Nothofagaceae) based on rDNA spacer sequence (ITS): taxonomic congruence with morphology and plastid sequence. *American Journal of Botany*, **84**, 1137–1155.

Marticorena, C. & Rodriguez, R. (2001) *Flora de Chile*. Universidad de Concepción, Concepción.

Melville, R. (1973) Continental drift and plant distribution. *Implications of continental drift for the Earth sciences* (ed. by D.H. Tarling and S.K. Runcorn), pp. 439–446. Academic Press, London.

Miller, A. (1976) The Climate of Chile. *Climates of Central and South America* (ed. by W. Schwerdtfeger), pp. 113–145. Elsevier Scientific Publishing Company, Amsterdam.

Romero, E.J. (1978) Paleoecología y paleofitogeografía de las tafofloras del Cenofítico de Argentina y áreas vecinas. *Ameghiniana*, **15**, 209–227.

Romero, E.J. (1986) Paleogene phytogeography and climatology of South America. *Annals of Missouri Botanical Garden*, **73**, 449–461.

Schmithüsen, J. (1956) Die räumliche Ordnung der chilenischen Vegetation. *Bonner Geographische Abhandlungen*, **17**, 1–86.

Selles, D. & Hinojosa, L.F. (1997) Niveles sedimentarios y paleofloras del Oligoceno superior-Mioceno inferior en la Formación Abanico, noreste de Santiago. *Congreso Geológico Chileno*, **8**, 580–584.

Sinnott, E.W. & Bailey, I.W. (1915) Foliar evidence as to the ancestry and early climatic environment of the angiosperms. *American Journal of Botany*, **2,** 1–22.

Tanai, T. (1986) Phytogeographic and phylogenetic history of the genus *Nothofagus* BL. (Fagaceae) in the southern hemisphere. *Journal of the Faculty of Science, Hokkaido University, Series IV*, **21**, 505–582.

Troncoso, A. (1991) Paleomegaflora de la formación Navidad, miembro Navidad (Mioceno), en el área de Matanzas, Chile central occidental. *Boletín Museo Nacional de Historia Natural, Chile*, **42**, 131–168.

Troncoso, A. & Romero, E.J. (1998) Evolución de las comunidades florísticas en el extremo sur de Sudamérica durante el Cenofítico. *Proceedings of the Congreso Latinoamericano de Botánica, N° 6* (ed. by R. Fortunato and N. Bacigalupo), pp. 149–172. Monographs in Systematic Botany, Missouri Botanical Garden.

Van Husen, C. (1967) Klimagliederung in Chile auf der basis von Häufigkeitsverteilungen der Niederschlagssummen. *Feriburger Geographische Hefte*, **4**, 0–113.

Villagrán, C. (1993) Una interpretación climática del registro palinológico del último ciclo glacial-postglacial en Sudamérica. *Bulletin de l'Institut Francais d'Études Andines*, **22**, 243–258.

Villagrán, C. (1995) Quaternary history of the Mediterranean vegetation of Chile. *Ecology and biogeography of Mediterranean ecosystem in Chile, California and Australia* (ed. by M. Kalin, R. Zedler and M. Fox), pp. 3–20. Springer-Verlag, New York.

Villagrán, C. (2001) Un modelo de la historia de la vegetación de la Cordillera de La Costa de Chile central-sur: la hipótesis glacial de Darwin. *Revista Chilena de Historia Natural*, **74**, 793–803.

Villagrán, C. & Armesto, J.J. (2005) Fitogeografía histórica de la Cordillera de la *Costa de Chile*. *Biodiversidad y ecología de los bosques de la Cordillera de la Costa de Chile* (ed. by C. Smith, J.J. Armesto and C. Valdovinos), pp. 99–116. Editorial Universitaria, Santiago.

Villagrán, C. & Hinojosa, L.F. (1997) Historia de los bosques del sur de Sudamérica, II: Análisis fitogeográfico. *Revista Chilena de Historia Natura*, **70**, 241–267.

Villagrán, C., Moreno, P.I. & Villa-Martinez, R. (1995) Antecedentes palinológicos acerca de la historia Cuaternaria de los bosques chilenos. *Ecología de los bosques nativos de Chile* (ed. by J.J. Armesto, C. Villagrán and M.T.K. Arroyo). Comité de Publicaciones Científicas, Vicerrectoría Académica, Universidad de Chile, Editorial Universitaria, Santiago.

Villagrán, C., Le-Quesne, C., Aravena, J.C., Jiménez, H. & Hinojosa, L.F. (1998) El rol de los cambios de clima del Cuaternario en la distribución actual de la vegetación de Chile central – sur. *Bamberg Geographische*, **15**, 227–242.

Wiemann, M.C., Manchester, S.R., Dilcher, D.L., Hinojosa, L.F. & Wheeler, E.A. (1998) Estimation of temperature and precipitation from morphological characters of dicotyledonous leaves. *American Journal of Botany*, **85,** 1796–1802.

Willis, J.C. (1985) *A dictionary of flowering plants and ferns*, 8th edn. Cambridge University Press, Cambridge.

Wolfe, J. (1979) Temperature parameters of humid to mesic forests of eastern Asia and relation to forests of other regions of the northern hemisphere and Australasia. *United States Geological Survey Professional Paper*, **1106**, 1–37.

Wolfe, J. (1993) A method of obtaining climatic parameters from leaf assemblages. *U. S Geological Survey Bulletin*, **2040**, 71.

Zachos, J., Pagani, M., Sloan, L., Thomas, E. & Billups, K. (2001) Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science*, **292**, 686–693.

SUPPLEMENTARY MATERIAL

The following supplementary material is available online from http://www.Blackwell-Synergy.com:

Table S1 Data set of morphological variables measured for each modern and fossil flora (according to Wolfe, 1993).

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