

Patagonian Vegetation Turnovers during the Paleogene-Early Neogene: Origin of Arid-Adapted Floras

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Abstract

The structure of the living Patagonian flora, dominated by the steppe, is a direct consequence of past climatic and tectonic events. These arid-adapted communities were widespread during the Late Neogene, but their origin in Patagonia can be traced back to the Paleogene. Vegetational trends throughout Paleocene-Miocene time are based on available paleobotanical and palynological information. Four major supported stages in vegetation turnovers are recognized: (1) Paleocene and Early Eocene floras were rainforest-dominated, including many angiosperms with warm-temperate affinities (e.g., palms, Juglandaceae, Casuarinaceae). However, mainly in the Early Eocene, some geographic areas influenced by warm but drier conditions are suggested by the occurrence of certain taxa (e.g., Anacardiaceae). These areas containing arid-adapted floras would have arisen in Patagonian inland regions, in a generally wet continent. (2) The Middle Eocene-Early Oligocene interval was distinguished by the invasion of *Nothofagus* forests. Progressive replacements of megathermal communities by meso- and microthermal rainforest are documented. *Nothofagus* forest expansion suggests a marked

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cooling trend at this time, although some megathermal elements (Aquifoliaceae *Ilex*, Tiliaceae-Bombacaceae, Sapindaceae) were still present at the beginning of this period. Arid-loving taxa have not been recorded in abundance. (3) Late Oligocene-Early Miocene floras were characterized by the occurrence of shrubby-herbaceous elements belonging to Asteraceae, Chenopodiaceae, Ephedraceae, Convolvulaceae, Fabaceae, and Poaceae. They began to give a modern appearance to plant communities. Xerophytic formations would have occupied coastal salt marshes and pockets in inland areas. Megathermal angiosperms of the Rubiaceae, Combretaceae, Sapindaceae, Chloranthaceae, and Arecaceae occurred mainly during the Late Oligocene. Forests of Nothofagaceae, Podocarpaceae, and Araucariaceae are still documented in extra-Andean Patagonia; however, a contrast between coastal and inland environments may have developed, particularly in the Miocene. (4) Middle-Late Miocene records show an increasing diversity and abundance of xerophytic-adapted taxa, including Asteraceae, Chenopodiaceae, and Convolvulaceae *Cressa/Wilsonia*. Expansion of these xerophytic taxa, coupled with extinctions of megathermal/nonseasonal elements, would have been associated with both tectonic and climatic forcing factors, led to the development of aridity and extreme seasonality. These arid-adapted Late Miocene floras are closely related to modern communities, with steppe widespread across extra-Andean Patagonia and forest restricted to the western humid upland regions.

Resumen

Principales tendencias de la vegetación en Patagonia durante el Paleógeno-Neógeno temprano: origen de las floras adaptadas a condiciones de aridez. La estructura de la flora patagónica actual, dominada por la estepa, es consecuencia directa de los eventos tectónicos y climáticos a los que ha estado sometida. Estas comunidades, adaptadas a condiciones de extrema aridez, se expandieron durante el Neógeno tardío, aunque su origen en Patagonia pudo haber ocurrido en el Paleógeno. En base a la información paleobotánica y palinológica disponible se sustentan las cuatro etapas principales de cambios en la vegetación a través del intervalo Paleoceno-Mioceno: 1- Paleoceno-Eoceno Temprano, con floras dominadas por selvas, incluyendo angiospermas con afinidades megatérmicas (ej. palmeras, Juglandaceae, Casuarinaceae). En el Eoceno Temprano, en algunas áreas geográficas habrían prevalecido condiciones cálidas pero áridas según surge de la presencia de taxones con estos requerimientos (ej. Anacardiaceae). Estos parches xerofíticos se habrían desarrollado en el interior de la Patagonia dentro de un entorno general húmedo. 2- Eoceno Medio-Oligoceno Temprano, caracterizado por la expansión de los bosques de *Nothofagus*. Se documentó un progresivo reemplazo de comunidades megatérmicas por bosques meso y microtéricos dominados por *Nothofagus* y podocarpaceas, indicando un marcado enfriamiento. Al principio de este intervalo, sin embargo, todavía se reconocen algunos elementos megatéricos (Aquifoliaceae *Ilex*, Tiliaceae-Bombacaceae, Sapindaceae); los taxones xerofíticos, en cambio, son muy escasos. 3- Oligoceno Tardío-Mioceno Temprano, determinado por la presencia de elementos herbáceo-arbustivos de Asteraceae, Chenopodiaceae, Ephedraceae, Convolvulaceae, Fabaceae, Poaceae, que empezaron a dar una apariencia moderna a las comunidades vegetales. Las formaciones xerofíticas habrían ocupado ambientes costeros como marismas o parches abiertos en áreas internas. Angiospermas megatéricas como Rubiaceae, Combretaceae, Sapindaceae, Chloranthaceae y Arecaceae están bien representadas, en particular en el Oligoceno Tardío. Los bosques de

Nothofagaceae, Podocarpaceae y Araucariaceae todavía estarían presentes en la Patagonia extra-andina, pero ya existiría un marcado contraste entre los ambientes continentales y costeros. 4- Mioceno Medio-Tardío, definido por un marcado incremento en la diversidad y abundancia de taxones xerófitos incluyendo Asteraceae, Chenopodiaceae y Convolvulaceae *Cressa/Wilsonia*. La expansión de estas formas y la extinción de elementos megatérmicos, no estacionales, habrían estado asociadas a factores tectónicos y climáticos que condujeron al desarrollo de aridez y extrema estacionalidad. Las floras áridas del Mioceno Tardío se encuentran estrechamente relacionadas con las comunidades modernas, con la estepa expandida en la Patagonia extra-andina y los bosques restringidos a la región húmeda, occidental, de los Andes.

Introduction

Patagonia is now cold and arid, and it has been characterized as one of the windiest regions in the world (average annual temperature, $\sim 12^{\circ}\text{C}$; annual rainfall, $\sim 300\text{mm}$). The flora is dominated by shrubs and herbs (steppe), with morphological and physiological features associated with such environmental stress. Only in western areas, close to the Andes, is rainfall high enough to allow the development of forests, with a dense understory of tree ferns, vines, and shrubs. The transformation to an arid-dominated landscape is fairly recent, and was probably reached after several paleogeographic, tectonic, and global paleoclimatic changes. The isolation of Antarctica by separation from Australia and South America caused a general trend toward cooler conditions and led to the development of a major ice sheet in Antarctica. The Patagonian Andes uplift produced an important orographic rain shadow to the east of this mountain belt during Miocene time (Blisniuk et al., 2005), causing a progressive increase in aridity and a reduction in the atmospheric CO_2 concentration (Willis & McElwain, 2002). All of these changes would have led to the expansion of a cooler and drier climate throughout the Patagonian landscape. A general global cooling trend has been recognized from the Late Eocene onward, but cold conditions were established by the Late Miocene (Zachos et al., 2001). Nevertheless, during the Late Oligocene and latest Early Miocene times, some warm stages have been recognized (Zachos et al., 2001). The vegetational history of Patagonia during the Cenozoic was achieved from analysis of available paleobotanical and palynological information. These data, however, are not homogeneous, since some temporal gaps without, or with only very scanty, information occur. The bulk of paleobotanical studies coming from Patagonia were originally published by Dusén (1907), Berry (1925, 1932, 1935a, 1935b, 1935c, 1937a, 1937b, 1938), and Hünicken (1955), but they have been challenged by new research, with some published results (Romero et al., 1988; Gandolfo et al., 1988, 2004; Gonzalez et al., 2002; Wilf et al., 2003, 2005) and some in progress. The first palynological studies were restricted to the Paleocene and Eocene sequences (Fasola, 1969; Freile, 1972; Archangelsky, 1972, 1973; Romero, 1977; Romero & Zamalao, 1985; Archangelsky & Zamalao, 1986). During recent decades, a great increase in palynological information, especially from Oligocene and Miocene deposits, has become available (Barreda, 1993, 1996, 1997a, 1997b, 1997c, 1997d, 1997e; Barreda & Palamarczuk, 2000a, 2000b, 2000c; Zamalao, 2000, 2004; Leanza et al., 2002; Barreda et al., 2003; Melendi et al., 2003; Guerin et al., 2004; Palazzesi & Barreda, 2004, 2005; Zamalao & Romero, 2005).

The origin and spread of arid-adapted communities throughout the Paleocene-Late

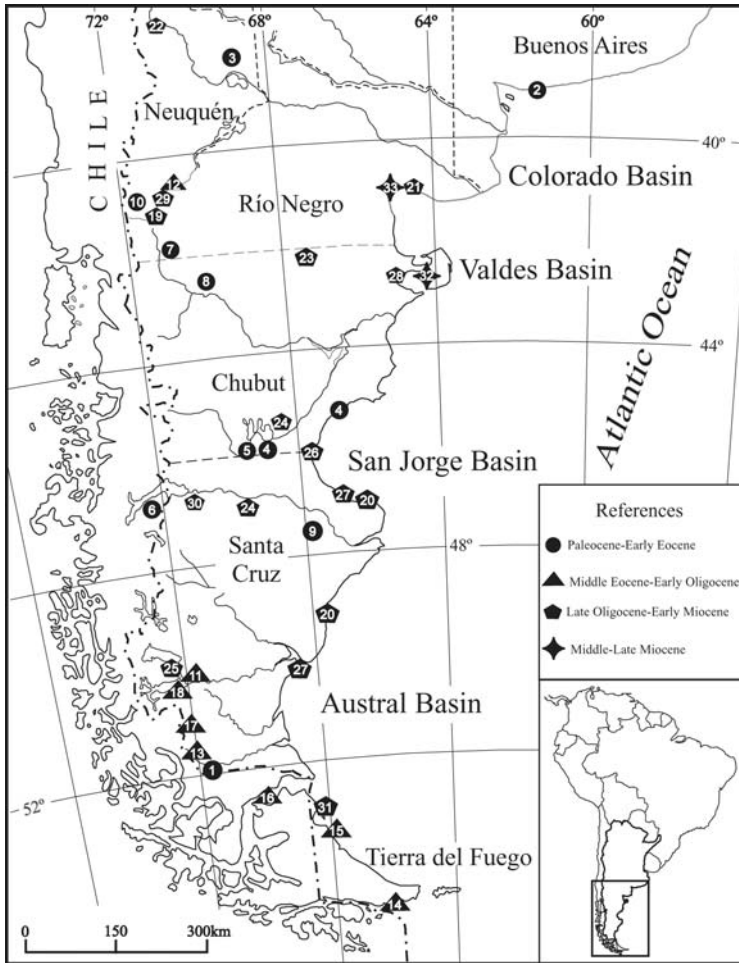


Fig. 1. Location map of paleobotanical and palynological sites. **Paleocene-Early Eocene:** 1. Cerro Dorotea Formation (Freile, 1972; Romero, 1973). 2. Pedro Luro Formation (Ruiz & Quattrocchio, 1997). 3. Jagüel Formation (Romero, 1973; Archangelsky & Romero, 1974a, 1974b; Barreda et al., 2004b). 4. Salamanca Formation (Romero, 1968, 1973; Petriella, 1972; Archangelsky, 1973, 1976; Archangelsky & Romero, 1974a, 1974b; Archangelsky & Zamaloa, 1986). 5. Flora de Cerro Funes (Berry, 1937a). 6. Ligorio Marquez Formation (Chile) (Suarez et al., 2000). 7. Laguna del Hunco Flora (Berry, 1925, 1935a, 1935b, 1935c; Frenguelli & Parodi, 1941; Frenguelli, 1943a, 1943b; Petersen, 1946; Traverso, 1964; Romero & Hickey, 1976; Durango de Cabrera & Romero, 1986; Romero et al., 1988; González et al., 2002; Wilf et al., 2003; Gandolfo et al., 2004). 8. Río Pichileufú Flora (Berry, 1938; González et al., 2002; Wilf et al., 2005). 9. Estancia Laguna Manantiales (Zamaloa & Andreis, 1995). 10. La Huitrera Formation (lower section) (Melendi et al., 2003). **Middle Eocene-Early Oligocene:** 11. Calafate Formation (Sepúlveda, 1980; Sepúlveda & Norris, 1982). 12. La Huitrera Formation (upper section) (Baez et al., 1990; Melendi et al., 2003). 13. Río Turbio Formation (Berry, 1937b; Hünicken, 1955; Archangelsky, 1972; Romero, 1977; Romero & Zamaloa, 1985; Romero & Castro, 1986; Ancibor, 1988, 1990; Brea, 1993). 14. Sloggett Formation (Olivero et al., 1998). 15. Estancia La Sara (Menéndez & Caccavari, 1975). 16. Loreto Formation (Fasola, 1969). 17. Río Guillermo Formation (Dusén, 1907; Frenguelli, 1941; Brandmayr, 1945; Hünicken, 1955). 18. Río Leona Formation (Dusén, 1907; Frenguelli, 1941; Brand-

Miocene interval in Patagonia are the main topic of this study, together with the major vegetation turns involved.

Materials and Methods

The analyzed interval is the Paleocene to Late Miocene, from 23.03 to 5.33 Ma, following the geological chart of Gradstein et al. (2004).

Classification of fossil pollen is based on its morphological characters (International Code of Botanical Nomenclature, Art. 1.2; Greuter et al., 2000). Pollen morphology may in part, but not entirely, reflect evolution within the groups of plants that produced the pollen. In this report, names of fossil pollen species are shown in parentheses to clearly distinguish them from the names of extant taxa. Neither fossil pollen nor leaves can always be assigned by morphology to their parent plants below the family level and sometimes not even at that level. The uncertainties are much higher in older sediments; thus, in this overview, all inferences are based on those taxa with defined affinities. The Patagonian vegetation trends are portrayed by analogy with modern taxa and their habitat preferences.

Plant response to major environmental variables such as light, temperature, and precipitation follows the classification of Nix (1982). The terms megathermal ($>24\text{ }^{\circ}\text{C}$), mesotherm ($>14\text{ }^{\circ}\text{C}$, $<20\text{ }^{\circ}\text{C}$), and microthermal ($<12\text{ }^{\circ}\text{C}$), with two interzones, are used instead of tropical, subtropical, warm temperate, and cool or cold temperate, because the latter terms have geographical connotations as well. These terms are widely used in discussing Cenozoic vegetational turns (Macphail et al., 1994, and references therein).

As the major changes in vegetation composition during the Cenozoic do not precisely fit the classic divisions of geologic time (Periods and Epochs), time intervals dependent on these floral changes have been used instead (e.g., Macphail et al., 1994; Graham, 1999; Martin, 2006). In Patagonia, four main intervals (Paleocene-Early Eocene, Middle Eocene-Early Oligocene, Late Oligocene-Early Miocene, and Middle-Late Miocene) have been defined in accordance with global (paleoclimate, paleogeography) and regional (Andes uplift, sea flooding) forcing factors (Barreda, 2002; Palazzesi and Barreda, in press).

Both the paleobotanical and palynological data here analyzed come from a vast area, ranging from 38°S to 54°S (Fig. 1). Owing to this wide latitudinal interval, only assemblages with comparable geographical positions can be compared with confidence.

Fig. 1. continued

mayr, 1945; Hünicken, 1955; Barreda et al., 2004a). **Late Oligocene-Early Miocene:** **19.** Río Foyel Formation (Pöthe de Baldis, 1984; Barreda et al., 2003). **20.** San Julián Formation (Pöthe de Baldis, 1974; Barreda, 1997e; Barreda & Palamarczuk, 2000a). **21.** Barranca Final Formation (Gamerro & Archangelsky, 1981; Guerstein, 1990a, 1990b, 1990c; Guerstein & Quattrocchio, 1988; Guerstein & Guler, 2000, Guler et al., 2001, 2002; Guler, 2003). **22.** Lileo Formation (Leanza et al., 2002). **23.** Sierra La Colonia locality (Archangelsky & Zamaloa, 2003). **24.** Sarmiento Formation (Spegazzini, 1924; Berry, 1932). **25.** Centinela Formation (Guerstein et al., 2004). **26.** Chenque Formation (Romero, 1970; Barreda, 1993, 1996, 1997a, 1997b, 1997c, 1997d; Barreda & Caccavari, 1992; Palamarczuk & Barreda, 1998). **27.** Monte León Formation (Barreda & Palamarczuk, 2000a, 2000b). **28.** Gaiman Formation (Palazzesi & Barreda, 2005). **29.** Ñirihau Formation (Fiori, 1939). **30.** Pinturas Formation (Zamaloa, 1993). **31.** Cullen Formation (Vergel & Durango de Cabrera, 1988; Zamaloa & Romero, 1990; Zetter et al., 1999; Zamaloa 2000, 2004; Zamaloa & Romero, 2005). **Middle-Late Miocene:** **32.** Puerto Madryn Formation (Palazzesi & Barreda, 2004, 2005). **33.** Río Negro Formation (Guler, 2003).

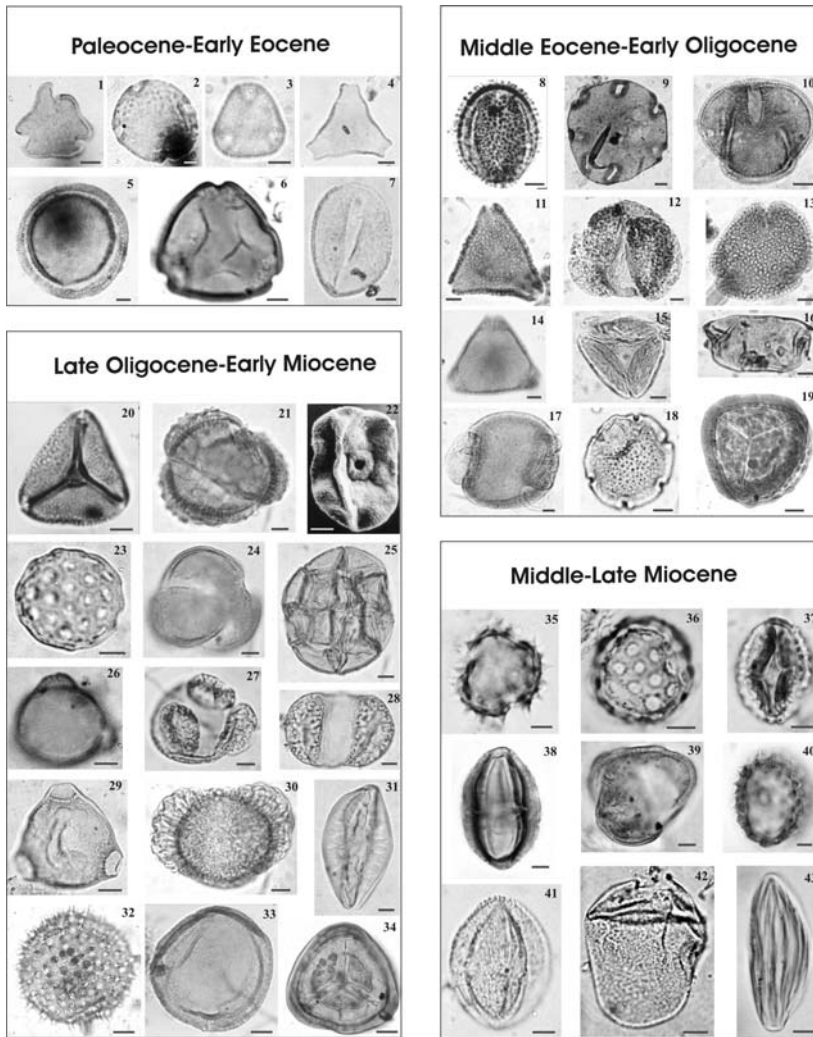


Fig. 2. Fossil pollen grains of the most significant taxa developed during Paleogene and Early Neogene times in Patagonia. **Paleocene-Early Eocene:** 1. Proteaceae (*Peninsulapollis gillii*). 2. Ulmaceae (*Ulmoideipites krempii*). 3. Olacaceae (*Anacolisidites* sp.). 4. Proteaceae (*Triatriopollenites lateflexus*). 5. (*Classopollis* sp.). 6. Juglandaceae (*Plicatopollis wodehousei*). 7. Arecaceae (*Monosulcites* sp.) (Specimens in 1, 2, and 5 are from the Jagüel Formation; 3, 4, and 7 are from the Salamanca Formation; and 6 is from the La Huitrera Formation, lower section). **Middle Eocene-Early Oligocene:** 8. Aquifoliaceae (*Ilex-pollenites cliffdenensis*). 9. Nothofagaceae *Nothofagus* (*Nothofagidites flemingii*). 10. Gunneraceae *Gunnera* (*Tricolpites reticulatus*). 11. Proteaceae *Lomatia* (*Proteacidites* sp.). 12. Podocarpaceae (*Podocarpidites* sp.). 13. Bombacaceae (*Intratriporopollenites* sp.). 14. Proteaceae (*Proteacidites* sp.). 15. Menyanthaceae (*Striasyncolpites laxus*). 16. Proteaceae *Embothrium* (*Diporites* sp.). 17. Podocarpaceae *Lagarostrobos franklinii* (*Phyllocladidites mawsonii*). 18. Nothofagaceae *Nothofagus* (*Nothofagidites acromegacanthus*). 19. Lophosoriaceae *Lophosoria* (*Cyatheacidites annulatus*). (Specimens in 8–14 and 17–19 are from the Río Turbio Formation, and 15 and 16 are from the Río Leona Formation). **Late Oligocene-Early Miocene:** 20. Sapindaceae *Cupania* (*Cupanieidites reticularis*). 21. Asteraceae

Results

The analysis of the available data from Patagonia supports the major stages of vegetational turnover defined for the Paleocene-Late Miocene interval. These stages represent distinctive floristic assemblages, both in composition and structure. Selected fossil pollen grains from each time interval are shown in Figure 2. Moreover, sketches of the major structures of Patagonian vegetation during each of the four inferred stages are shown in Figure 3. The present results are only provisional as not all floras are well dated in Patagonia; most of them, however, can be related to an accurate biostratigraphic scheme.

PALEOCENE-EARLY EOCENE

The warmest climatic conditions of the Cenozoic occurred during the Paleocene-Early Eocene interval, and a particularly low equator-to-polar temperature gradient has been recognized (Willis & McElwain, 2002). The vegetation was markedly diverse and adapted to the warm climatic conditions. A marked expansion of megathermal angiosperms toward middle and high latitudes has been documented, mainly during the Early Eocene.

The following analyzed data are from both paleobotanical and palynological sources (Fig. 1). Paleocene outcrops of the Jagüel (northwestern Patagonia), Salamanca (east central Patagonia), and Cerro Dorotea (southwestern Patagonia) formations, and fragmentary cutting samples, obtained by drilling, from the Pedro Luro Formation (northeastern Patagonia), provide records about the Danian (Early Paleocene) vegetation (Berry, 1937a; Romero, 1968, 1973; Freile, 1972; Petriella, 1972; Archangelsky 1973, 1976; Archangelsky & Romero, 1974a, 1974b; Petriella & Archangelsky, 1975; Archangelsky & Zamaloa, 1986; Ruiz & Quattrocchio, 1997; Barreda et al., 2004b). Age control of these units is based on dinoflagellate cysts and foraminifera (Malumián & Caramés, 1995, 1997; Quattrocchio & Sarjeant, 1996; Ruiz & Quattrocchio, 1997; Palamarczuk, 2004). Neither paleobotanical nor palynological information is available from the Late Paleocene of Argentina. In southern Chile (46°S), however, there are data from the Late Paleocene-?Early Eocene from the Ligorio Márquez Formation (Suarez et al., 2000). Early-Middle Eocene data are abundant, with the Laguna del Hunco and Río Pichileufú floras being the most representative of northwestern Patagonia. These floras

Fig. 2. continued

Mutisiae (*Mutisiapollis viteauensis*). 22. Poaceae (*Graminidites* sp.). 23. Chenopodiaceae (*Chenopodipollis chenopodiaceoides*). 24. Convolvulaceae *Cressa/Wilsonia* (*Tricolpites trioblatus*). 25. Fabaceae *Acacia* (*Acaciapollenites myrtosporites*). 26. Casuarinaceae (*Haloragacidites trioratus*). 27. Podocarpaceae *Myrcrocachrys* (*Microcachrydites antarcticus*). 28. Podocarpaceae *Podocarpus* (*Podocarpidites* sp.). 29. Onagraceae *Epilobium* (*Corsiniipollenites atlantica*). 30. Podocarpaceae *Dacrydium* (*Lygistipollenites florinii*). 31. Ephedraceae *Ephedra* (*Equisetosporites claricristatus*). 32. Malvaceae (*Baumannipollis chubutensis*). 33. Araucariaceae *Araucaria* (*Araucariacites australis*). 34. Lophosoriaceae *Lophosoria* (*Cyatheacidites annulatus*). (Specimen in 20 is from the San Julián Formation; those in 21–25 and 27–34 are from the Chenque Formation; and that in 26 is from the Gaiman Formation). **Middle-Late Miocene.** 35. Asteraceae (*Tubulifloridites antipodica*). 36. Chenopodiaceae (*Chenopodipollis* sp.). 37. Asteraceae (*Tubulifloridites pleistocenicus*). 38. Asteraceae (*Mutisiapollis* sp.). 39. Convolvulaceae *Cressa/Wilsonia* (*Tricolpites trioblatus*). 40. Malvaceae (*Baumannipollis* sp.). 41. Anacardiaceae (*Striatricolporites* sp.). 42. Cyperaceae (*Cyperaceapollis neogenicus*). Ephedraceae *Ephedra* (*Equisetosporites notensis*). 43. Ephedraceae *Ephedra* (*Equisetosporites notensis*). (Specimens in 35–43 are from the Puerto Madryn Formation). Scale bar = 5 µm, except in 19, 29, and 32–34, where the scale bar = 10 µm.

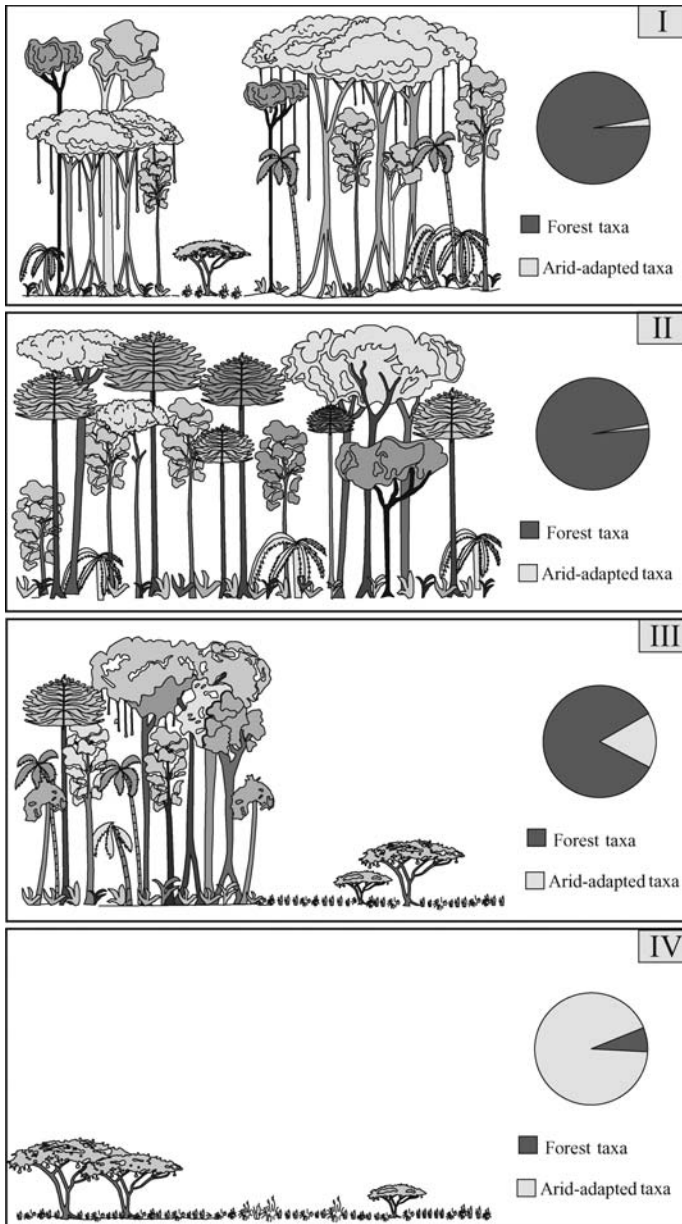


Fig. 3. Major structures of the Patagonian vegetation represented by four landscape sketches of the temporal intervals herein proposed: (1) Paleocene-Early Eocene; (2) Middle Eocene-Early Oligocene; (3) Late Oligocene-Early Miocene; and (4) Middle-Late Miocene. Although these reconstructions are not strictly quantitative, they are based on the major groups represented in each time interval. Pie graphs show the average percentages from the available quantitative information (Archangelsky, 1976; Romero, 1977; Barreda, 1996, 1997e; Olivero et al., 1998; Melendi et al., 2003; Palazzesi & Barreda, 2004).

have long been investigated by Berry (1925, 1935a, 1935b, 1935c, 1938), and new species descriptions and overviews have been published (Frenguelli & Parodi, 1941; Frenguelli, 1943a, 1943b; Petersen, 1946; Traverso, 1964; Romero & Hickey, 1976; Argüjio & Romero, 1981; Aragón & Romero, 1984; Durango de Cabrera & Romero, 1986; Gandolfo et al., 1988; Romero et al., 1988; González et al., 2002). Recent isotopic data indicate $\text{Ar}^{40}/\text{Ar}^{39}$ ages of 51.91 ± 0.22 Ma (Early Eocene) for the Laguna del Hunco and 47.46 ± 0.05 Ma (Middle Eocene) for the Río Pichileufú floras (Wilf et al., 2005). Some paleobotanical data also come from the Cerro Funes locality (Berry, 1937a). Well-preserved Early Eocene palynological assemblages have been described from the La Huitrera Formation (lower section), at the Nahuel Huapi Este locality. The only age control was provided by spore-pollen assemblages (Melendi et al., 2003). Moreover, a little information comes from outcrops in the Estancia Laguna Manantiales area, southeastern Patagonia (Zamaloa & Andreis, 1995). The age of this last section is not accurately known, but is probably Early-Middle Eocene.

Early Paleocene floras from northern and central Patagonia were gymnosperm-dominated, the morphotaxon *Classopollis* being the most important element (Archangelsky, 1973; Ruiz & Quattrocchio, 1997; Barreda et al., 2004b). Neotropical megathermal taxa were abundant, with the occurrence of Olacaceae *Anacolosa* (*Anacolosidites* sp.), Arecaceae *Nypa* (*Spinozonocolpites* sp.) and (*Palmoxylon patagonicum*), Ulmaceae (*Ulmoideipites* sp.), Pandanaceae *Pandanus* (*Pandaniidites* sp.), and Symplocaceae *Symplocos* (*Senipites* sp.). Southern Gondwanic lineages were represented by Podocarpaceae, Araucariaceae, Cunionaceae, and Proteaceae. Regional climate is interpreted as warm and humid, with mangrove communities developing in coastal environments of Chubut (Petriella, 1972; Archangelsky, 1973; Petriella & Archangelsky, 1975; Archangelsky & Zamaloa, 1986). The scarce information from southernmost Patagonia indicates the presence of some megathermal families (Olacaceae *Anacolosa*), along with Myrtaceae and Proteaceae (Freile, 1972). Very scarce pollen grains of Nothofagaceae have been reported from Paleocene formations (Romero, 1973; Archangelsky & Romero, 1974b), and no macrofossil remains have been recorded so far.

Late Paleocene-Early Eocene data from the Ligorio Márques Formation (Chile) indicate a significant diversity of megathermal Lauraceae (Suarez et al., 2000) suggesting that warm conditions prevailed even in southern Patagonia. Other megathermal flora of broad-leaved character comprising Lauraceae, Sterculiaceae, and Vitaceae has been described from the Cerro Funes locality (Berry, 1937a).

Eocene paleobotanical information from central Patagonia indicates high plant diversity (Wilf et al., 2003, 2005), with the presence of megathermal families (palms, Myrtaceae *Myrcia*, Sapindaceae *Schmidelia* and *Cupania*, Lauraceae, Rubiaceae *Coprosma*, and Casuarinaceae *Gymnostoma*). Their presence suggests an equable climate with winter mean temperatures warmer than 10 °C and abundant rainfall (Wilf et al., 2003, 2005; Gandolfo et al., 2004). Other taxa with broader climatic requirements from these formations include conifers, cycads, and Ginkgoales (among gymnosperms), along with Proteaceae *Lomatia* and Malvales. Arid-adapted elements of Anacardiaceae (*Striatricolporites* sp.), Celtidaceae *Celtis*, and Fabaceae Caesalpinoideae *Cassia* have been reported in some geographic areas (Hünicken, 1955; Wilf et al., 2003, 2005). The first Poaceae macrofossil remains in Patagonia, of *Chusquea* affinity (tall Bambusoideae grasses), are also recorded (Frenguelli & Parodi, 1941). Spore-pollen assemblages are dominated by Podocarpaceae, Araucariaceae, Proteaceae (*Beauprea*), and megathermal

Juglandaceae (*Plicatopollis* spp.). A comparable association, but further south, has been reported from the Estancia Laguna Manantiales, with high frequencies of megathermal taxa related to Juglandaceae (*Plicatopollis* sp.), Tiliaceae-Bombacaceae (*Intratripopollenites* sp.), Chloranthaceae (*Clavatipollenites* sp.), and Arecaceae (*Proxapertites* sp.) (Zamaloa & Andreis, 1995).

No evidence of Nothofagacean forests in the Patagonian vegetation has been reported for this interval, although such forests were widespread in the Antarctic Peninsula (Askin, 1990).

MIDDLE EOCENE-EARLY OLIGOCENE

A progressive temperature decrease with an expansion of temperate to cold temperate biomes characterized this second, Middle Eocene-Early Oligocene time interval. A major change in the composition of the flora in Patagonia was supported by a marked increase in abundance and diversity of meso- to microthermal clades, *Nothofagus* being the most prominent example.

Middle-Late Eocene data come from outcrops of the La Huitrera (northwestern Patagonia, near Confluencia), Río Turbio, and Calafate (southwestern Patagonia) formations and cutting samples from Estancia La Sara well (southernmost Patagonia) (Berry, 1937b; Hünicken, 1955; Archangelsky, 1972; Menéndez & Caccavari, 1975; Romero, 1977; Sepúlveda & Norris, 1982; Romero & Zamaloa, 1985; Romero & Castro, 1986; Ancibor, 1988, 1990; Baez et al., 1990; Brea, 1993; Melendi et al., 2003). Late Eocene to earliest Oligocene is represented by the Sloggett (southernmost Argentina, south of 54°S) and Loreto (southern Chile, 53°S) formations (Fasola, 1969; Olivero et al., 1998). Early Oligocene data were provided by the Río Guillermo and Río Leona (southwestern Patagonia) formations (Dusén, 1907; Frenguelli, 1941; Brandmayr, 1945; Hünicken, 1955; Barreda et al., 2004a). The temporal position of these formations was inferred from their palynological content (Archangelsky, 1968, 1969; Menéndez & Caccavari, 1975; Melendi et al., 2003).

Paleobotanical and palynological assemblages recovered from Middle-Late Eocene sequences indicate the invasion of *Nothofagus* forests. Evidence from northern and southern Patagonian records shows that this expansion coincided with the occurrence of other micro- to mesothermal families such as Podocarpaceae, Araucariaceae, Myrtaceae, Cunoniaceae, Gunneraceae, Caryophyllaceae, and Proteaceae. The diversity of Proteaceae was higher in northern Patagonia, with elements probably related to the extant *Beauprea* and *Symphyonema* (Melendi et al., 2003). Megathermal families of the Lauraceae, Tiliaceae-Bombacaceae, Malpighiaceae, Sapindaceae, Rubiaceae, and Aquifoliaceae *Ilex* have been documented as well (Hünicken, 1955; Romero & Zamaloa, 1985; Romero & Castro, 1986; Melendi et al., 2003). In southern Patagonia, Berry (1937b) reported the presence of a small monocotyledonous fragment that he referred to as Poaceae from the Río Turbio Formation. Even though this assignment needs further investigation, the coeval presence of phytolith remains related to grasses (Andreis, 1972; Zucol & Brea, 2005) supports Berry's determination. A seasonal climate has been suggested for this area by the occurrence of distinct growth rings in fossil Nothofagaceae wood (Brea, 1993).

During the latest Eocene-Early Oligocene an expansion of micro- to mesothermal taxa occurred, and no records of megathermal elements have been documented so far. Assemblages were fairly homogeneous in composition, dominated by developing

forests of Nothofagaceae, Podocarpaceae, Araucariaceae, Cunoniaceae *Weinmannia*, and Proteaceae *Lomatia* and *Embothrium* (Fasola, 1969; Olivero et al., 1998; Barreda et al., 2004a). The understory would have been composed of ferns (Polypodiaceae, Lophosoriaceae, Schizaeaceae) and herbs (Gunneraceae, Menyanthaceae [*Striasyncolpites laxus*]), indicating a high rainfall regime and temperate to cold-temperate climatic conditions. Evidence for aridity is scanty, at least in southern Patagonia, and restricted solely to the presence of Anacardiaceae.

LATE OLIGOCENE-EARLY MIOCENE

During the Late Oligocene-Early Miocene interval, new warming episodes allowed the expansion of megathermal and mesothermal angiosperms at middle-high latitudes of Patagonia. Late Oligocene-Early Miocene was a transition time in the vegetation structure, from one dominated by forests to one in which shrubby and herbaceous elements became progressively important. Moreover, the first records of some shrubby and herbaceous elements in southern South America are found, Asteraceae and Convolvulaceae *Cressa/Wilsonia* being the most important taxa.

Late Oligocene data are scarce and come from outcrops of the San Julián Formation, southeastern Patagonia (Pöthe de Baldis, 1974; Barreda, 1997e; Barreda & Palamarczuk, 2000b). Pollen assemblages from the Río Foyel Formation (northwestern area) are probably coeval or slightly older (Pöthe de Baldis, 1984; Barreda et al., 2003).

Early-Middle Miocene palynological data are relatively abundant, with records from the Lileo, Barranca Final, Gaiman, Chenque, Monte León, Centinela, Pinturas, and Cullen formations (Fig. 1), occupying a wide latitudinal area (Gamerro & Archangelsky, 1981; Guerstein & Quattrocchio, 1988; Vergel & Durango de Cabrera, 1988; Guerstein, 1990a, 1990b, 1990c; Zamalao & Romero, 1990; Barreda & Caccavari, 1992; Zamalao, 1993, 2000, 2004; Barreda, 1993, 1996, 1997a, 1997b, 1997c, 1997d; Malumíán et al., 1998; Palamarczuk & Barreda, 1998, 2000; Zetter et al., 1999; Barreda & Palamarczuk, 2000a, 2000b, 2000c; Guerstein & Guler, 2000; Guerstein & Junciel, 2001; Leanza et al., 2002; Guler & Guerstein, 2002; Guerstein et al., 2004; Palazzesi & Barreda, 2005; Zamalao & Romero, 2005). Age control of these units is based mainly on dinoflagellate cysts and foraminifera content. $\text{Sr}^{87}/\text{Sr}^{86}$ ages based on bivalve shells indicate an Early Miocene (Aquitanian) age for the Centinela Formation (Casadío et al., 2001). $\text{Ar}^{40}/\text{Ar}^{39}$ determinations from the top of the Monte León Formation also indicate an Early Miocene age (19.2 Ma) (Feagle et al., 1995). Palynological information also comes from the Sierra La Colonia locality (Fig. 1), central Chubut province (Archangelsky & Zamalao, 2003).

Paleobotanical data are scanty for the whole interval, restricted to leaf imprints and woody remains from Ñirihuau and Chenque formations (Fiori, 1939; Romero, 1970). There are also reports from the Cañadón Hondo (Berry, 1932) and Deseado River (Spegazzini, 1924) localities; both reports refer to the Sarmiento Formation.

Late Oligocene floras are dominated by forests of Podocarpaceae, Nothofagaceae, and Araucariaceae, with abundant ferns of the Lophosoriaceae *Lophosoria*, Pteridaceae *Pteris*, and Polypodiaceae *Polypodium*, and megathermal angiosperms of the Arecaceae, Malpighiaceae, Rubiaceae *Gardenia*, Combretaceae *Combretum/Terminalia*, Sapindaceae *Cupania*, and Chloranthaceae in lowland areas (Barreda, 1997e, Barreda & Palamarczuk, 2000a). Gunneraceae and Onagraceae *Fuschsia* have also been reported. Shoreline communities include the first Asteraceae Mutisiae and Convolvulaceae (*Tri-*

colpites asperamarginis), along with Poaceae, Chenopodiaceae, and Ephedraceae, but in lower frequencies. Herbaceous and shrubby elements were not recorded in the Río Foyel Formation, though.

Late Oligocene-Miocene assemblages from northwestern Patagonia (Lileo Formation) suggest that forests were dominant (Podocarpaceae, Nothofagaceae, Araucariaceae), with scarce herbaceous taxa of the Onagraceae and Restionaceae. Fossil Poaceae leaves have been reported from the Ñirihuau Formation (Fiori, 1939).

During the Early Miocene (early Aquitanian), the first expansion of shrubby elements of the Chenopodiaceae, Ephedraceae, and Convolvulaceae *Cressa/Wilsonia* occurred. Grasses also occurred, but in low frequencies. Forests were dominated by southern elements of the Podocarpaceae, Nothofagaceae, and Araucariaceae, with fern communities. Megathermal Arecaceae, Symplocaceae *Symplocos*, and Lauraceae (*Ulmium atlanticum*) are still documented in central Patagonia, but they were scanty in the southernmost region (Romero, 1970; Barreda, 1993, 1996). The presence of Nothofagacean megafossils has also been reported from the Sarmiento Formation in the Cañadón Hondo and Deseado River areas (Spegazzini, 1924; Berry, 1932). Swamp communities, dominated by Sparganiaceae (Archangelsky & Zamaloa, 2003), are recognized in central Patagonia (Sierra La Colonia locality). These communities appear to be Early Miocene in age, based on the presence of some stratigraphic markers: Asteraceae (*Mutisiapollis viteauensis*), Convolvulaceae *Cressa/Wilsonia* (*Tricolpites trioblatus*), and Poaceae (Barreda, pers. observ.). Forests seem not to be developed nearby the swamp region considering the low frequencies of Nothofagaceae and Podocarpaceae observed. These pollen assemblages might reflect vegetation growing in the swamp margins and represent local rather than regional communities.

In the late Early Miocene (Late Aquitanian), drier conditions would have prevailed in lowland areas, considering the abundance of Ephedraceae and Chenopodiaceae and the presence of some sclerophyllous trees of the Casuarinaceae *Casuarina*, Fabaceae Mimosoideae *Acacia* (*Acaciapollenites myriosporites*), *Anadenanthera* (*Polyadopollenites* sp.), Caesalpinoideae *Caesalpinia* (*Margocolporites vanwijhei*), and Proteaceae *Banksia*. The contraction of humid elements, such as the Podocarpaceae (e.g., *Dacrydium*, *Lagarostrobos*), coincides with the expansion of xerophytic taxa. Rainforest trees, however, contributed to pollen assemblages and may have developed riparian or gallery forests in central Patagonia.

The latest Early Miocene (Burdigalian) was marked by a new increase in megathermal Sapindaceae *Cupania* and Euphorbiaceae *Alchornea*. Aquatic herbs and hydrophytes such as Cyperaceae, Sparganiaceae, Restionaceae, and Malvaceae (*Baumannipollis chubutensis*) were dominant. Tree ferns of the Cyatheaceae *Cyathea* were also abundant. Coastal salt marshes and dry pockets in inland areas were occupied by Chenopodiaceae, Convolvulaceae, and Asteraceae (Barreda, 1996; Barreda & Palamarczuk, 2000b); Ephedraceae decreased in frequency, though. Forests remained across extra-Andean Patagonia until about the Middle Miocene.

MIDDLE-LATE MIOCENE

The rise in importance of shrubby and herbaceous elements, determined by a cooling and drying trend across extra-Andean Patagonia, began to give a modern appearance to the landscape during the Middle-Late Miocene.

The expansion of xerophytic-adapted taxa, coupled with the demise of the last

megathermal taxa, characterize this stage. Rainforest elements recognized during the Late Oligocene and Early Miocene became rare or extinct toward the Late Miocene.

Records from the Middle-Late Miocene are limited to palynological evidence. Data come from the Barranca Final, Río Negro, and Puerto Madryn formations in northeastern Patagonia (Guler et al., 2001, 2002; Guler, 2003, Palazzesi & Barreda, 2004). $\text{Sr}^{87}/\text{Sr}^{86}$ ages based on pectinid shells indicate a Late Miocene age (10 Ma) for the Puerto Madryn Formation (Scasso et al., 2001). These data coincide with a previous $\text{K}^{40}/\text{Ar}^{40}$ age determination from volcanic tuff (Zinsmeister et al., 1981). Age control from the Barranca Final Formation was established on the basis of foraminifera (Malumián et al., 1998), whereas a date from the Río Negro Formation was based on its palynological content.

Spore/pollen assemblages are dominated by angiosperms, mainly shrubby and herbaceous taxa of the Chenopodiaceae, Convolvulaceae *Cressa/Wilsonia*, and Asteraceae. Malvaceae, Anacardiaceae, Fabaceae, and Poaceae are recognized as well, along with Cyperaceae, Sparganiaceae/Typhaceae, and Restionaceae. Gymnosperms are mainly represented by Ephedraceae, while Podocarpaceae and Araucariaceae are scarce. Floating ferns belonging to Azollaceae are abundant at some levels. Other pteridophytes and bryophytes are uncommon, being poorly represented by a few species (Barreda et al., in press).

No direct Late Miocene palynological data from the southern Andean region have been reported so far, but mesothermal to microthermal forests would have prevailed according to pollen records from eastern areas, in which *Nothofagus fusca* pollen is the major element.

Discussion and Conclusion

Forests would have been widespread in the Paleogene of Patagonia within areas now occupied by steppe. They have even been documented in the earliest Neogene in the extra-Andean region, on the basis of both palynological and paleobotanical evidence. The rise of the first xerophytic pockets can be traced back to the Paleogene, though. Some taxa may have originated within Patagonian rainforest communities and later adapted to locally dry sites. Others may have reached Patagonia by dispersal events and then become important with the spread of dry environments during the Miocene.

The Paleocene-Early Eocene interval was rainforest dominated. It was marked, mainly in the Early Eocene, by highly diverse vegetation, with abundant megathermal elements. The occurrences of Anacardiaceae, Celtidaceae *Celtis*, and Fabaceae *Cassia* during Eocene time support the existence of local areas dominated by shrubs and low trees and adapted to more arid conditions in a generally wet continent. The oldest fossil Poaceae remains in Patagonia were dated as Early-Middle Eocene, in agreement with the oldest megafossil record of the family known worldwide (Jacobs et al., 1999). One of these taxa was interpreted to be *Chusquea* (Frenguelli & Parodi, 1941), a member of Bambusoideae, today occurring in the understory of rainforests in southwestern Patagonia. Recent silicophytolith findings in the Sarmiento Formation (Puesto Almendra Member), central Patagonia (Zucol & Brea, 2005), agree with the finding of such plant communities developing in the Patagonian rainforest during the Eocene. However, no Eocene pollen evidence has been reported so far, and other earlier Poaceae reports (Berry, 1937b) need confirmation. Drought stress conditions in north-central Patagonia are indicated by the presence of evaporites and calcareous paleosols in the early Eocene

Gran Salitral Formation (Melchor et al., 2002), suggesting a warm semiarid climate with a mean annual temperature higher than 20 °C. Bellosi et al. (2002) also reported tuffaceous paleosols calcretized through pedogenesis in the Sarmiento Formation. Volcanism, which began to spread from the Eocene onward, may have played a major role as a regional forcing factor on both composition and vegetation structure. Ash soils would have been drier niches to be occupied by xerophytic taxa. Moreover, from the Eocene onward, warm intervals were characterized by a progressive increase in the number of taxa that today are frequent in the dry seasonal forests of tropical South America (Chaqueño Domain) such as Anacardiaceae and Bombacaceae (Prado & Gibbs, 1993).

The Middle Eocene-Early Oligocene vegetation was marked by the irruption of *Nothofagus* forests. The expansion of this group suggests a marked cooling trend at this time, although some megathermal elements (Aquifoliaceae *Ilex*, Tiliaceae-Bombacaceae, Sapindaceae) were still present at the beginning of this stage. Juglandaceae and Aquifoliaceae became extinct at these high latitudes at the end of the Eocene, and they are not recorded during later warm episodes. Latest Eocene-Early Oligocene fossil floras from southern Patagonia indicate the development of temperate forests containing Gondwanic lineages (Nothofagaceae, Podocarpaceae, Araucariaceae), without records of well-defined megathermal elements. Xerophytic taxa were not abundant during Middle-Late Eocene or Early Oligocene time, based on paleobotanical and palynological fossil records.

By the Late Oligocene-Early Miocene, warm climates allowed the dispersal of neotropical elements southward (palms, *Cupania*, *Alchornea*, Rubiaceae, Combretaceae), adding megathermal elements to the local Gondwanic floras. The rise of xerophytic and halophytic shrubby-herbaceous elements (Convolvulaceae, Asteraceae, Poaceae, Chenopodiaceae, Ephedraceae) during the Late Oligocene to importance in the Early Miocene began to give a modern appearance to plant communities. Xerophytic associations probably occupied coastal salt environments and pockets in inland areas. Riparian or gallery forests, however, were still present in extra-Andean Patagonia. Although grasses are recorded, pollen frequencies are not high enough to suggest grasslands.

During the Early Miocene, distinctive elements of the Chaco Domain increased (Anacardiaceae *Schinus*, Fabaceae *Caesalpinia* and *Anadenanthera*, Combretaceae *Combretum*), and some of them may have grown in gallery forests.

The Middle-Late Miocene was characterized by the final demise of megathermal elements in Patagonia, coupled with an increasing diversity and abundance of xerophytic-adapted taxa, including Asteraceae, Chenopodiaceae, and Convolvulaceae *Cressa*/*Wilsonia*. These changes would have been associated with both tectonic and climatic forcing factors. Pollen records of Poaceae were still scarce in the Late Miocene. Available data from carbon isotope ratios of fossil tooth enamel and phytolith studies indicate that from the Late Miocene onward there was a major expansion of grass-dominated communities in southern South America (Latorre et al., 1997; Jacobs et al., 1999). Asteraceae are well documented in the Patagonian fossil record, and became abundant and diverse during the Late Miocene. Among the recorded taxa during this time are several identified morphotypes related to Mutisieae (Mutisiinae, Nassauviinae), Heliantheae (*Ambrosia*), and Barnadesioideae (Barreda et al., 2006). The low frequencies observed of Podocarpaceae and Nothofagaceae pollen types during the Late Miocene across extra-Andean Patagonia indicate that these taxa would have grown a considerable

distance from the coast. These arboreal pollen grains may have been transported long distances from the west (e.g., close to the Andean region). Late Miocene vegetation was similar to the present vegetation, with the steppe expanded across extra-Andean Patagonia and the forest restricted to western areas where rainfall was still abundant.

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