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High Plant Diversity in Eocene South America: Evidence from Patagonia

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Tropical South America has the highest plant diversity of any region today, but this richness is usually characterized as a geologically recent development (Neogene or Pleistocene). From caldera-lake beds exposed at Laguna del Hunco in Patagonia, Argentina, paleolatitude ~47°S, we report 102 leaf species. Radioisotopic and paleomagnetic analyses indicate that the flora was deposited 52 million years ago, the time of the early Eocene climatic optimum, when tropical plant taxa and warm, equable climates reached middle latitudes of both hemispheres. Adjusted for sample size, observed richness exceeds that of any other Eocene leaf flora, supporting an ancient history of high plant diversity in warm areas of South America.

There is little evidence but much debate regarding how long the exceptional plant diversity of tropical South America has existed (*1*, *2*). Most explanations have emphasized the late Neogene or Pleistocene (*3*–*7*), although the mechanisms and relative importance of geologically recent speciation are disputed (*8*–*12*). Evidence for or against earlier diversity is sparse (*13*–*17*). During the early Eocene, when maximum global temperatures for the Cenozoic occurred (*18*, *19*), plants with tropical affinities grew at middle and high latitudes (*20*–*23*). From quantitative sampling of a middle-latitude flora, we present evidence for extraordinary plant diversity in early Eocene South America.

The flora we studied comes from the vicinity of Laguna del Hunco (LH) in northwestern Chubut Province, Patagonia, Argentina (*24*, *25*). It is derived from tuffaceous caldera-lake deposits, known as the Tufolitas Laguna del Hunco, of the middle Chubut River volcanic-pyroclastic complex (*25*, *26*). Previous K/Ar analyses of associated volcanic rocks have indicated a late Paleocene to middle Eocene age for the flora (*27*, *28*). Marine sediments in nearby basins and tectonic evidence suggest that elevation was low and that the climate had a maritime influence (*29*, *30*). The site is near the southern limit of the Paleogene Neotropical flora (*20*, *21*, *23*), and it also contains a number of taxa that are extinct in South America today but have living relatives in Australasian floras (*31*–*33*) (Fig. 1).

We measured and correlated stratigraphic sections through the Tufolitas LH that contained 25 fossil localities, three datable tuffs, and six paleomagnetic reversals (Fig. 2) (*34*). We identified 1536 specimens of compression-impression plant macrofossils; nearly all (98%) were found between the 37- and 99-m levels of the aggregate systems (Fig. 2). Four quarries were selected for intensive sampling (64% of specimens) (Fig. 2).

Results from $^{40}Ar/^{39}Ar$ analyses of the tuffs indicated ages near 52 Ma (million years ago) (Fig. 2) (*34*). The two youngest ages are at odds with superposition, but their confidence intervals either overlap or nearly overlap each other's means. From paleomagnetic results, we assign the most fossiliferous strata to the upper portion of magnetic polarity subchron (C) 23n.2r and the lower half of C23n.2n (Fig. 2) (*34*). These data place the flora within the early Eocene climatic optimum (EECO), an ~2-million-year interval that is known for the warmest sustained temperatures of the Cenozoic (*19*). At 52 Ma, the latitude of LH was ~47° to 48°S (*35*).

In the flora, we recognize 102 leaf species (includes described species and undescribed morphospecies) of dicots, monocots, conifers, ginkgophytes, cycads, and ferns and an addi-

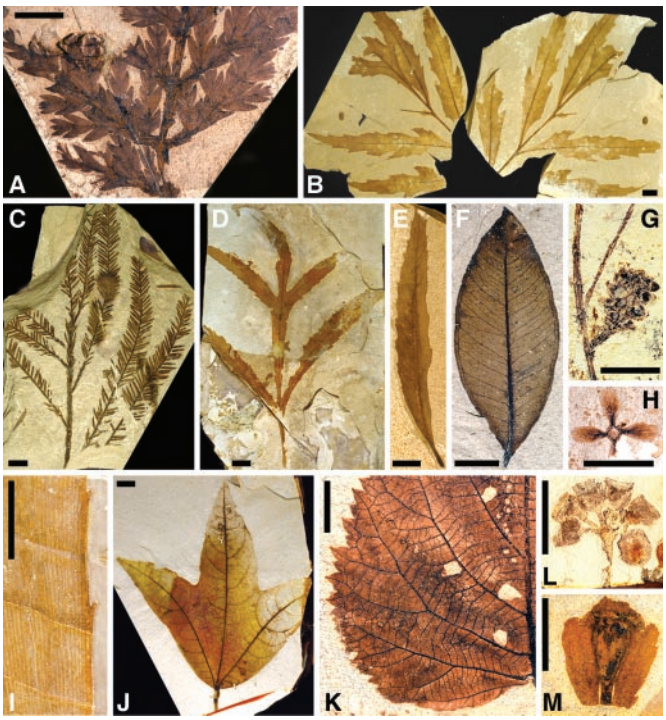


Fig. 1. Selected plant taxa representing the excellent preservation and taxonomic and morphological diversity of the Laguna del Hunco flora (*33*, *36*). Scale bars, 1 cm. Parentheses indicate Museo Egidio Feruglio (MEF) specimen number and locality (Fig. 2). (**A**) Attached foliage of callitroid Cupressaceae similar to extant *Austrocedrus* (South America) and to several Australasian genera (MEF 971, loc. 13). (**B**) Attached compound leaf of "*Lomatia*" *preferruginea* (Proteaceae), part and counterpart, with lobed and toothed leaflets (972, 15). (**C**) Shoot and attached foliage of Podocarpaceae (973, 15). At least three other species of podocarps were found. (**D**) Complete, pinnatifid leaf of *Lomatia occidentalis* (Proteaceae) (974, float specimen). (**E**) "*Myrica*" *mira*, leaf (affinity unknown), with distinctive paired teeth along margin (975, 13). (**F**) Myrtaceae, leaf, showing prominent intramarginal vein (976, 13). (**G**) Attached infructescence and leaf of *Gymnostoma* sp. (Casuarinaceae, extant in Australasia). Note exserted bracts of infructescence and grooved surface of the nodular leaf (977, 22). (**H**) Propeller-like fruit, with four persistent sepals, of an unknown dicot species (?Cunoniaceae), with constricted sepal bases and thickened central disk (978, 6). (**I**) Cycad leaf similar to extant *Dioon*, with toothed margin (470, 4). (**J**) Malvales, three-lobed leaf, with basally actinodromous primary veins (979, 11). (**K**) Leaf-margin detail of unknown dicot species "TY62," showing compound, sharp-pointed teeth with flexuous or convex flanks and chevroned, opposite-percurrent tertiaries (980, 15). (**L**) Myrtaceae, infructescence (981, float specimen). (**M**) *Araucaria* sp. (Araucariaceae), attached seed and cone scale (982, 13). *Araucaria* foliage and a second type of cone scale were also found.

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tional 22 reproductive species from these groups (Fig. 1) (*33*, *34*, *36*). Dicots were the most diverse group, with 88 leaf species.

To evaluate species diversity relative to sample size, we derived rarefaction curves from relative abundance data of dicot leaves for the four most heavily sampled quarries, both individually (Fig. 3A) and in combination (Fig. 3B), as well as for the bulk flora (Fig. 3B). For comparison, we rarefied leaf counts for six Eocene floras from lacustrine and fluvial settings at middle paleolatitudes of western North America (Fig. 3). These six are diverse, well studied, and quantitatively sampled in a manner similar to the sampling at LH. The total known diversity of some of the North American floras is much greater than indicated by rarefaction analyses, but this reflects selective sampling of unknown numbers of specimens over years or decades (*37*–*39*).

None of the North American floras provides a precise temporal and depositional analog to the LH flora, but they represent similar age (Wyoming floras), topographic and depositional setting (Republic, Green River, Florissant), or maritime climate (Puget Group, Chalk Bluffs) (legend to Fig. 3). The Green River and Florissant floras are known for preservation of attached plant organs (*37*). No Eocene North American floras are available from caldera lakes, a setting that might favor the preservation of plant diversity because of steep surrounding topography (*38*, *40*). However, topography surrounding the caldera lake at LH was more subdued than it was to the south (*25*), and even in lake basins with high relief, remains of plants from elevated areas are rare (*41*). The most reliable comparisons are those with single quarries from fossil lakes (Fig. 3A, Republic, Green River, and Florissant). The combined quarries (Fig. 3B) introduce varying amounts of temporal and spatial mixing that may increase diversity artifactually, with perhaps the greatest effect in the Puget Group (*42*).

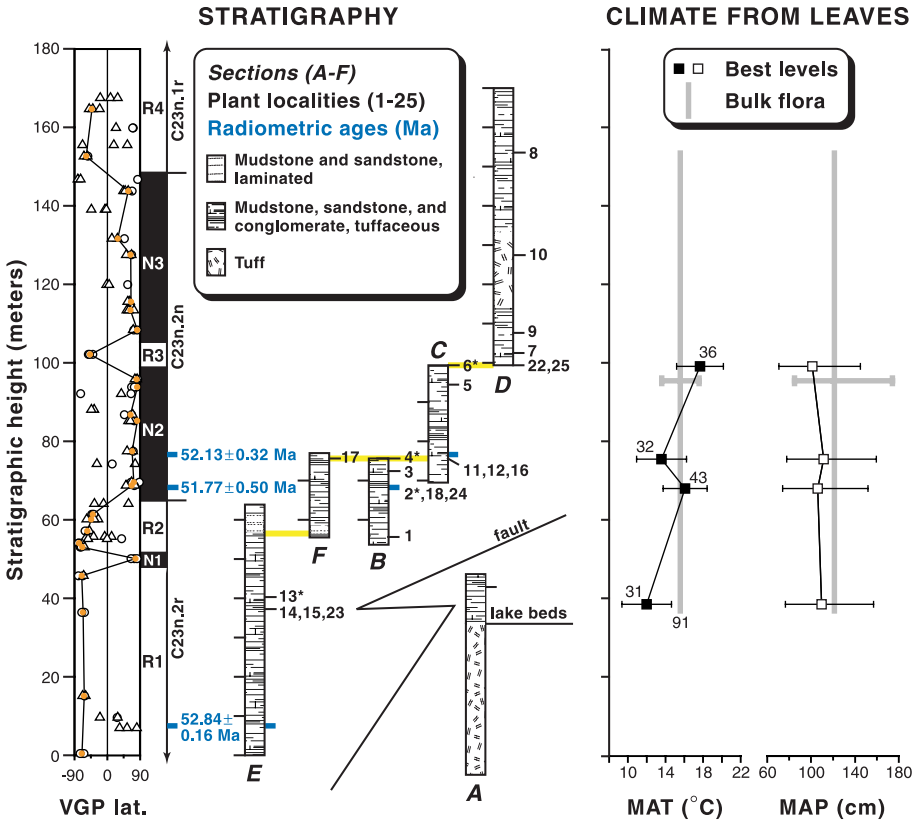


Fig. 2. Stratigraphic section of the Tufolitas Laguna del Hunco, aggregate thickness 170 m, showing principal lithologies; six local sections; correlations (yellow) along marker beds for the five continuous sections (B to F); plant localities; radiometrically dated samples, with 95% confidence intervals; virtual geomagnetic pole latitudes (VGP lat.); intervals of reversed and normal polarity (R1, N1, etc.), assignments to magnetic polarity subchrons (we interpret the single-site reversals, N1 and R3, as unidentified cryptochrons of short duration); and climatic results from leaf-margin (MAT) and leaf-area (MAP) analyses (*34*). The base of the Tufolitas LH was found only in section A, which could not be traced accurately across a fault to continuous sections B to F; these sections were measured on outcrops extending 1.3 km along a single drainage and were correlated by bed tracing. Section A is placed at an artificially high position in the figure (*34*). Most plant fossils occurred in tuffaceous mudrocks (*34*). Asterisks, the four principal quarries (see text and Fig. 3A). Red circles with connecting line, means of three individually measured, oriented paleomagnetic samples per site for which circular standard deviation was <35°. Open circles, paleomagnetic sample means calculated by principal components analysis (*59*). Open triangles, sample means calculated by Fisher statistics (*60*). Labels show the number of species used in the estimates for both MAT and MAP. MAT error bars indicate ±1σ of binomial error or ±2°C, whichever is greater (*46*); MAP error bars are ±1σ (*47*). Climatic results for the "best levels" include species from principal quarries and ancillary quarries excavated along strike (*34*). Bulk estimates include four species found only in float rocks not assignable to a precise stratigraphic level (*34*). Plant locality 19, not in a measurable position, is not shown.

The rarefaction analyses show that the LH flora is significantly more rich for its sample size than any Eocene leaf flora from North America (Fig. 3). Three of the four principal quarries from LH plot above (quarry 2) or within the 95% confidence limits of the most diverse North American localities (Fig. 3A). The same high diversity is apparent in rarefactions of the bulk flora and for subsets of the principal quarries (Fig. 3B). Nearly the same rarefaction curves result if the most diverse LH locality is removed (not shown). Thus, the elevated diversity observed at LH does not depend on a single locality or on the aggregation of numerous localities. Total richness also significantly exceeds that known from Eocene leaf floras of Germany (*43*), Australia (*44*), and Tanzania (*45*).

The mean annual temperature (MAT) estimated from leaf-margin analysis (*34*, *46*) of the bulk flora is 15.6° ± 2.0°C (Fig. 2). Individual sampling levels suggest an overall warming of ~6°C (from ~12° to 18°C), although we place the greatest confidence in the bulk estimate because of the large number of species used (Fig. 2). Mean annual precipitation (MAP) is estimated from leaf-area analysis (*47*) as 100 to 120 cm, with no evidence of significant change within the sampled interval (Fig. 2) (*34*). This estimate should be taken as a minimum: The high diversity of the flora suggests that the upper ranges of leaf size for many rare species are not yet sampled, and transport into lakes generally selects against large leaves (*48*). The combined presence of palms, cycads, araucarian conifers, diverse podocarps, and *Gymnostoma* (Fig. 1), along with the absence of *Nothofagus*, provide evidence of an equable climate, with winter temperatures warmer than ~10°C and abundant rainfall (*20*, *22*, *32*, *49*–*51*).

The precipitation proxies indicate that the Patagonian Andes to the west of LH did not cast a significant rain shadow, supporting other evidence for their low elevation (*29*, *52*). Our temperature data are corroborated by estimated sea-surface temperatures of 16° to 17°C during the EECO at four deep-sea sites from similar paleolatitudes in the South Atlantic (*53*). Marine and terrestrial proxy data from the Antarctic and from areas north of LH indicate temperatures that bracket our results latitudinally (*53*–*55*). Our estimated paleotemperatures for LH are

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less than or approximately equal to most of the North American sites, and precipitation estimates are also mostly comparable (legend to Fig. 3). Thus, climate biases against or is neutral with regard to our observation of relatively high species richness at LH (*56*, *57*).

Other evidence also is consistent with elevated floral diversity in Paleogene South America. The Eocene flora of Río Pichileufú, from ~160 km NNW of LH, contains many of the same species as the LH flora and appears to be as diverse (*33*, *58*), which suggests that rich, subtropical vegetation existed over a large portion of Eocene Patagonia. Palynological data from the Paleocene and Eocene of Colombia and Venezuela show significant diversification in association with warming temperatures and increased rainfall across the Paleocene-Eocene boundary, which suggests in situ speciation (*16*, *17*). Finally, numerous plant families that are now speciose in South America have Paleocene and Eocene fossil records there (*13*, *15*, *21*), demonstrating persistence and suggesting early diversification.

The current richness of South American floras has resulted from many factors, which include immigration, isolation, low extinction rates, and natural selection related to climate change and orogeny. These have been used to hypothesize a late Cenozoic origin of high Neotropical diversity, but our results suggest that elevated plant diversity is an ancient feature of South America.

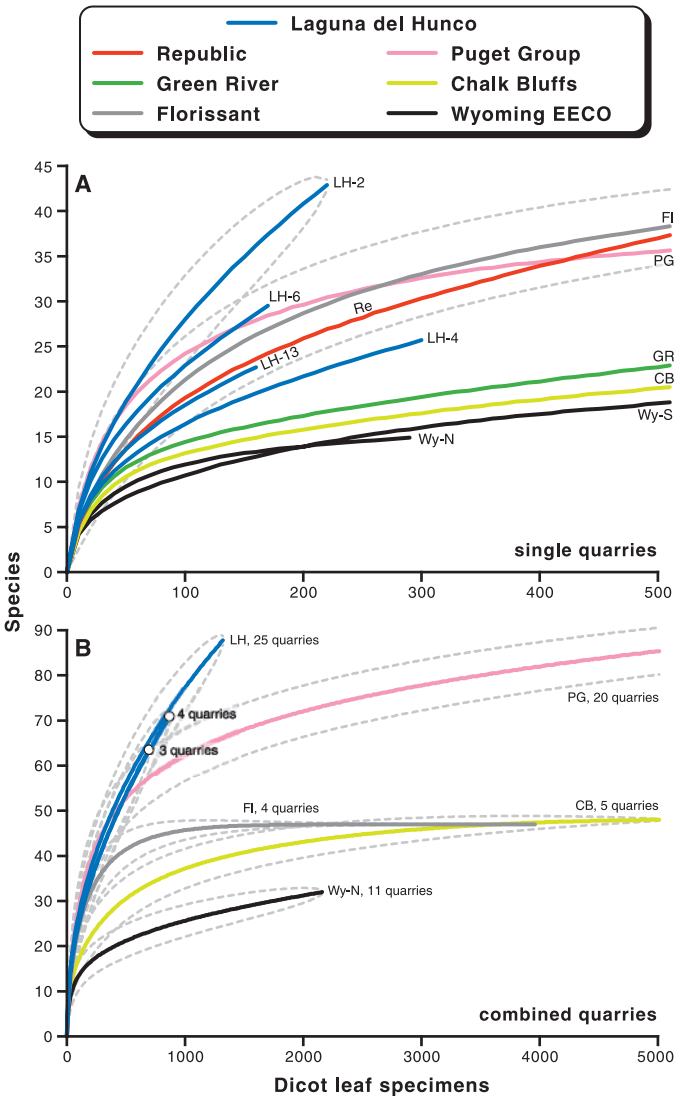


Fig. 3. Rarefied richness of dicot leaf species at Laguna del Hunco and quantitatively sampled sites from the Eocene of North America. Left column in key and LH flora are lacustrine assemblages; right column is fluvially deposited floras. Dashed gray lines, 95% confidence intervals. Leaf-count data (*33*): Republic (*61*); Green River (*62*); Florissant (*63*); Puget Group (*42*, *64*); Chalk Bluffs (*65*); Wyoming EECO (*66*, *67*). (**A**) Single-quarry collections, labeled with abbreviations corresponding to the key, shown up to 500 specimens for detail and including all four principal localities for Laguna del Hunco (Fig. 2, asterisks). Wy-N and Wy-S label samples from northern (*66*) and southern (*67*) Wyoming, respectively. For North American floras with data from more than one locality, only the most diverse quarry is shown, and confidence intervals are given, for readability, only for the most diverse samples from LH and North America (Florissant). (**B**) Lumped counts of three or more quarries from a single area, as labeled and shown up to 5000 specimens. For LH, rarefactions are shown for all 25 quarries, for the four principal quarries as in (A), and for the three uppermost principal quarries (LH-2, 4, and 6). Rarefactions computed using Analytic Rarefaction 1.3, by S. Holland (*68*). Ages, geologic settings, and estimated MATs and MAPs (if available) from leaf-margin and leaf-area analysis; climatic estimates are adjusted from published values in some cases so that all MATs and MAPs in this paper are derived using the identical formulae (*34*): Republic, Washington, 49 to 50 Ma lake in volcanic highlands, ~13°C (*61*, *69*); Green River flora (sample from Bonanza, Utah), ~43 to 48 Ma intermontane lake, ~15°C, ~84 cm (*47*, *70*–*72*); Florissant, Colorado, ~34 Ma montane lake, ~12° to 13°C (*37*, *63*, *73*, *74*); Puget Group flora, Washington, middle to late Eocene delta plain, ~16°C (*42*); Chalk Bluffs, California, 49 to 50 Ma fluvial system, ~17°C, ~160 cm (*47*, *65*, *72*, *75*); Wyoming EECO, ~53 Ma swamps and distal splays, ~21° to 22°C, ~140 cm (*18*, *66*, *67*).

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inspection of type material from the Eocene Río Pichileufú flora (*58*) confirms the reported taxonomic similarity to the LH flora (*26*), and our preliminary field data from Río Pichileufú suggest a diversity comparable to LH. Formal taxonomic knowledge of the LH flora is not yet sufficient to allow rigorous analysis of familial and generic diversity (*34*, *36*). All 1215 voucher specimens for this study are housed at MEF, including exemplar specimens of each species. Fieldwork reported here took place in November 1999. We do not attempt to integrate our data with previous collections in the United States and Argentina, which would be inappropriate for our stratigraphic methodology.

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Supporting Online Material

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Carotenoid Modulation of Immune Function and Sexual Attractiveness in Zebra Finches

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One hypothesis for why females in many animal species frequently prefer to mate with the most elaborately ornamented males predicts that availability of carotenoid pigments is a potentially limiting factor for both ornament expression and immune function. An implicit assumption of this hypothesis is that males that can afford to produce more elaborate carotenoid-dependent displays must be healthier individuals with superior immunocompetence. However, whether variation in circulating carotenoid levels causes variation in both immune function and sexual attractiveness has not been determined in any species. In this study, we show that manipulation of dietary carotenoid supply invokes parallel changes in cell-mediated immune function and sexual attractiveness in male zebra finches (*Taeniopygia guttata*).

Females in many animal species frequently prefer to mate with the most elaborately ornamented males (*1*), but how such displays reveal a male's worth is a contentious issue (*2*–*5*). For a signal to honestly reveal an individual's quality, it must be costly to produce (*6*, *7*). The expression of many ornamental traits depends on carotenoids, red and yellow pigments that animals cannot synthesize de novo and ultimately must obtain through their diet (*2*–*5*). Carotenoids are antioxidants and immunostimulants (*8*, *9*), and it has recently been hypothesized that a trade-off exists in carotenoid allocation between maintaining health and ornamentation: Males in better condition should require fewer carotenoids for immune function and could therefore use more of this resource to enhance ornamental display, thereby advertising their superior health (*10*, *11*). However, whether variation in

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