Cenozoic Plant Diversity in the Neotropics
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part of the spindle matrix in mitosis. Indeed, the yeast nuclear protein FIN1p contains coiled-coil domains and associates with spindles during mitosis (*46*). Furthermore, purified FIN1p self-assembles into 10-nm filaments resembling the cytoskeletal intermediate filaments formed in vitro (*46*).

In interphase nuclei of vertebrate cells, LB is concentrated at the nuclear lamina and is also distributed throughout the nucleoplasm. During interphase, the lamins interact with a wide range of nuclear proteins to regulate many nuclear functions as well as nuclear structural integrity. At the onset of mitosis, lamins are phosphorylated by Cdk1, which leads to the disassembly of nuclear lamina (*48*, *49*). The prevailing idea is that the disassembled LB is dispersed throughout the cytoplasm during mitosis. However, a fraction of LB is associated with the mitotic spindle and/or mitotic chromosomes (*19*, *26–28*). Our studies suggest that LB might perform functions analogous to those of the nuclear lamina to regulate spindle integrity and chromosome organization in mitosis.

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Cenozoic Plant Diversity in the Neotropics

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Several mechanisms have been proposed to explain the high levels of plant diversity in the Neotropics today, but little is known about diversification patterns of Neotropical floras through geological time. Here, we present the longest time series compiled for palynological plant diversity of the Neotropics (15 stratigraphic sections, 1530 samples, 1411 morphospecies, and 287,736 occurrences) from the Paleocene to the early Miocene (65 to 20 million years ago) in central Colombia and western Venezuela. The record shows a low-diversity Paleocene flora, a significantly more diverse early to middle Eocene flora exceeding Holocene levels, and a decline in diversity at the end of the Eocene and early Oligocene. A good correlation between diversity fluctuations and changes in global temperature was found, suggesting that tropical climate change may be directly driving the observed diversity pattern. Alternatively, the good correspondence may result from the control that climate exerts on the area available for tropical plants to grow.

The tropics of South America hold the highest plant diversity in the world (*1*). However, the origin of this diversity remains elusive. Many mechanisms have been proposed to explain it (*2–4*), which range from a long history of low rates of extinction and high rates of origination (*5*) to recent diversification during Pleistocene glacial-interglacial times (*6*). In particular, the latter mechanism [the "refugia" model (*6*)] is highly controversial and has ambiguous paleobotanical support (*7–11*). Despite the need for paleobotanical data to test Pleistocene and earlier models of diversification, the fossil record is deficient (*12–14*). Here, we present a high-resolution pollen and spore diversity record from the Paleogene to early Neogene in the Neotropics that shows that plant diversity in the tropics is variable through time and correlates with long-term global climatic changes.

The composite section. We analyzed the pollen and spore content from 15 stratigraphic sections in central Colombia and western Venezuela, spanning an area of 180,000 km^2 [Fig. 1; table S1; (*15*)]. The study encompassed 1530 palynological samples, recording 287,736 individual occurrences and 1411 morphospecies, 411 of which are still unnamed (*15*). The sections, as a whole, contain sediments that accumulated in fluvial to coastal plain settings between the Campanian and the middle Miocene [a range of 66 million years (My), from 82 to 16 million years ago (Ma)].

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Samples from all sections were combined in a single composite section by the method of graphic correlation (*15*, *16*). Each part of the composite section contains information from at least five different sections located across the entire study area. This procedure reduces the chance that differences in areas sampled influence apparent changes in taxonomic diversity over time, an effect commonly observed in continental-scale paleodiversity analyses (*17*).

The dating of the composite section was done by using foraminifera calibration points (*18*, *19*), stable carbon isotope ($\delta^{13}C$) stratigraphy (*15*), and key biostratigraphic datums (*15*). We assumed a linear sedimentation rate between these points in the composite section to transfer the stratigraphic position of each sample from meters to geologic time. It is reasonable to assume linearity, because the composite does not have major stratigraphic breaks and because diversity values are not affected by this assumption.

The composite section spans 66 My (*15*). The mean gap-sample resolution is 0.043 My; 95% of the samples are less than 0.150 My apart, and the longest sample gap is 0.586 My. Edge effects (*20*) artificially increase the number of first appearance datums (FADs) at the oldest end of a section and the number of last appearance datums (LADs) at the youngest end of a section. We estimated the edge effect by performing a piecewise regression (*15*, *21*). All data at both extremes of the composite that had evidence of an edge effect were eliminated from the analysis (the oldest 17.4 My and the youngest 3.3 My), which restricted the composite section from the base of the Paleocene (65.5 My) to the earliest Miocene (20 My). All species with single occurrences (39% of all species) were eliminated from the analysis. Last, the range-through method (*22*) was used to decrease the bias produced by changes in facies and depositional environments within the composite section. Six Holocene sediment cores with palynological data from lowland tropical forests of Colombia (*23*) were combined to produce a diversity benchmark to compare the Paleogene–early Neogene record with Holocene palynofloras (*15*). Because the pollen taxonomic resolution bias in both data sets is similar, their palynological diversity values are comparable. The six cores span an area similar to the area covered by our study, about 250,000 km^2. Samples from each of the cores were reduced to a single sample to replicate the time condensation that a rock sample may have. All of the core samples were combined to have a single composite sample that is comparable to a single data point in the long-term record shown here. This analysis yielded 321 pollen and spore morphotypes (*15*). A rarefaction analysis was also conducted to compare within-sample diversity between the Holocene palynofloras and the Eocene and early Miocene floras (*15*).

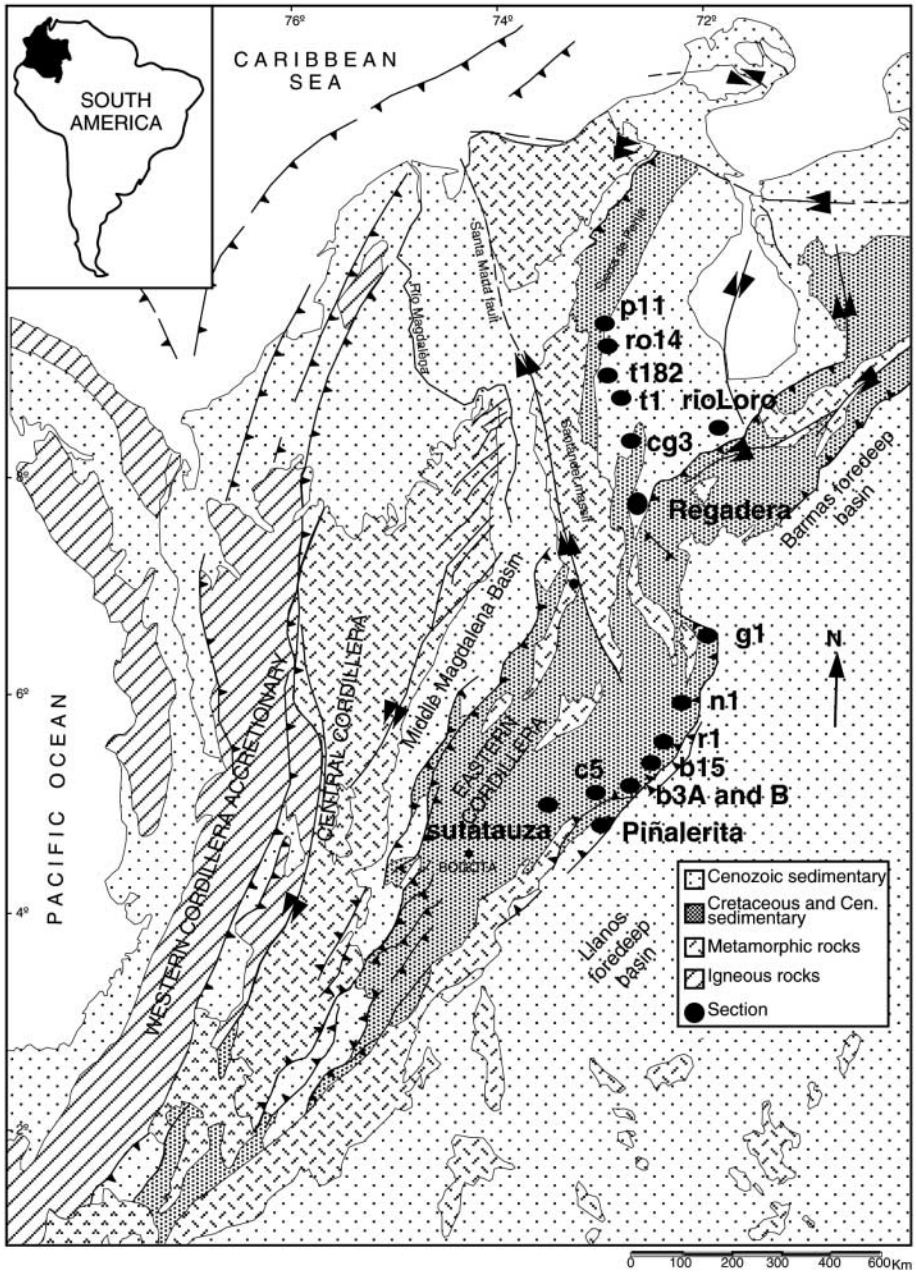

Fig. 1. Geographical location of the studied sections. Map modified after (*45*).

Standing diversity. The pattern of standing diversity (defined in the original sense of number of species) shows low floral diversity during the early Paleocene, followed by a slight increase at the beginning of the late Paleocene and by a subsequent drop in diversity at the end of the late Paleocene (Fig. 2A). Our composite record shows that a steady and fast increase in diversity occurred during the early Eocene, with a peak during the middle Eocene. This increase in Eocene diversity has already been suggested for subtropical South America, Africa, and India, although long-term records have not been yet published (*21*, *24*, *25*). Our record also shows a decline in diversity starting by the late middle Eocene with a steady drop until the early Oligocene. A similar drop has also been suggested for Southeast Asia during this time (*24*). Our record also indicates a relatively stable diversity during the Oligocene, followed by a slight decline during the Oligocene-Miocene transition (Fig. 2A).

Changes in floral composition were assessed using both a detrended correspondence analysis and an agglomerative cluster analysis (Fig. 2, B and C). Both methods show three significantly different floras: a Paleocene low-diversity flora, an early to early late Eocene high-diversity flora, and a mid-diversity late Eocene to early Miocene flora.

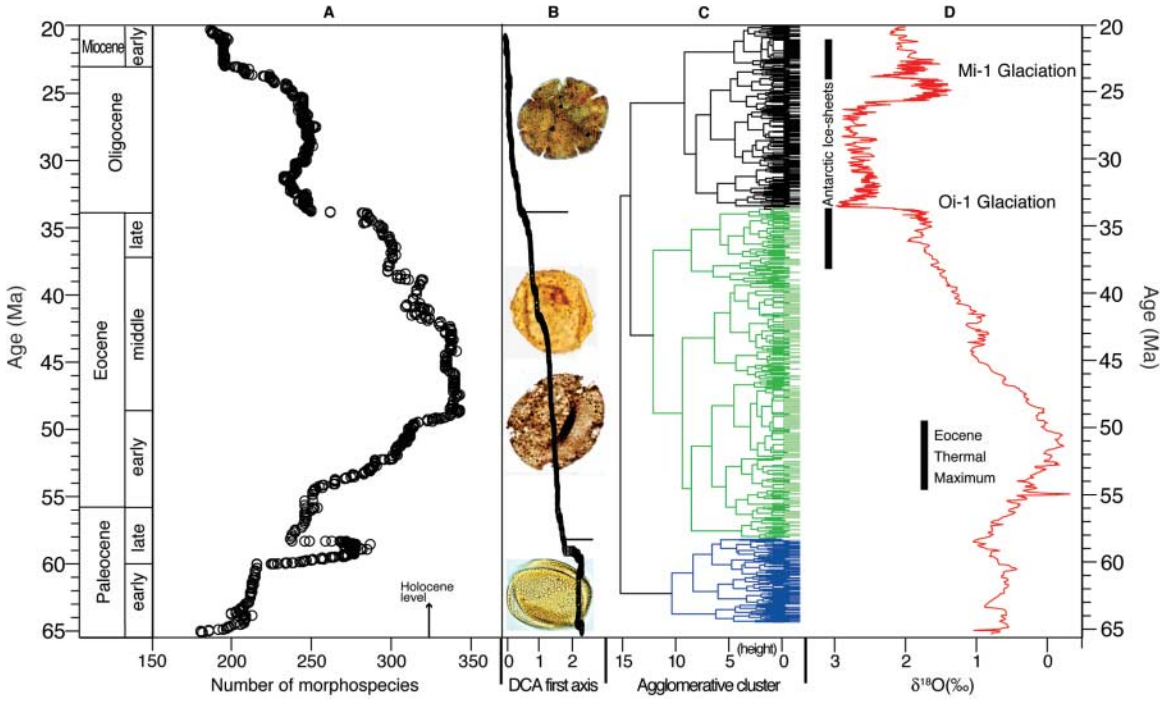

Fig. 2. Changes in palynofloral diversity and composition during the early to middle Cenozoic (*15*). (**A**) Pollen and spore standing diversity calculated by using the range-through method (*15*) and eliminating single-occurrence species. A Holocene composite palynological sample (*15*) of 321 species is drawn as a benchmark. Notice that diversity steadily increases during the early Eocene and gradually decreases during the late middle Eocene to early Oligocene, with a large drop at the Eocene-Oligocene boundary. (**B**) First axis of a detrended correspondence analysis (*15*) that explains 45.9% of the total variance in species composition along the stratigraphic profile. Paleocene palynofloras are clearly different from Eocene to Miocene palynofloras. Characteristic pollen species of each flora are shown: *Proxapertites cursus* for the Paleocene, *Nothofagidites huertasii* and *Echitriporites trianguliformis orbicularis* for the Eocene, and *Jandufouria seamrogiformis* for the Oligocene to early Miocene. (**C**) Agglomerative cluster analysis (*15*), showing three distinct palynofloras: Paleocene, Eocene, and Oligocene to early Miocene. (**D**) Global oxygen isotope curve for the Cenozoic (*27*). Raw data were smoothed using a five-point running average. There is correspondence between the general trend of the diversity curve and the global oxygen isotope curve that is a proxy for average global temperature (*27*).

Origination and extinction rates. Rates of origination and extinction were calculated by using the per capita rates of Foote (*15*, *20*) (Fig. 3). The rate of extinction is stable through time with an increase over background levels during the Eocene-Oligocene transition (Fig. 3A). Although the rate of origination gradually decreased over time (Fig. 3B), an increase over background levels occurred during the early Eocene (Fig. 3B). A high rate of both origination and extinction is apparent at the late Paleocene (Fig. 3, A and B). In fact, many of the species that originated at the beginning of the late Paleocene became extinct by the end of the Paleocene. There is also a major floral turnover at the end of the late Paleocene (Fig. 2, B and C). This interval needs further investigation to establish whether this extinction was gradual, or if it, in fact, dates from the short-lived Paleocene-Eocene thermal maximum and represents a rapid turnover as seen in North American mammals (*26*).

Standing diversity and global temperature. There is a correspondence between the global temperature curve for the Cenozoic (*27*) and the diversity pattern shown here [Fig. 2, A and D, first-differencing correlation of diversity versus $\delta^{18}O$, Spearman rho of –0.508; $P < 0.023$ (*15*)]. The increasing temperature trend from the early Paleocene to the early Eocene thermal maximum is paralleled, although slightly offset, by an increase in floral diversity. The subsequent long drop in temperature (*27*) between the late middle Eocene and the early Oligocene is also paralleled by a similar drop in diversity, with a larger drop in both temperature and diversity at the Eocene-Oligocene boundary (Fig. 2). This correspondence between diversity patterns and global temperature suggests a causal relationship. However, climate change at the tropics per se may not explain the differences seen here, because there is no strong evidence indicating that climate in the lowland tropics changed significantly during the Paleogene. The few available data of Cenozoic climate in the lowlands of the Neotropics indicate that temperature and precipitation may have been similar to modern values (*28*–*32*). However, these results are controversial, because the marine record seems to show a warming of the Tropics (*33*). The floral record also mimics recently estimated atmospheric CO_2 concentrations, which appear to be coupled with global temperature during the Paleogene (*34*). A gradual decrease in the partial pressure of atmospheric carbon dioxide (pCO_2) from the middle Eocene to the late Oligocene was identified from stable carbon isotope values of di-unsaturated alkenones from deep-sea cores (*34*). However, the pCO_2 proxies, based on plant stomatal indices, indicate that atmospheric CO_2 concentrations were near present-day levels during the Eocene (*35*). This conflicting evidence precludes a better understanding of the role of CO_2 on the pattern shown here.

Species-area effect. An alternative explanation to climate change in the Neotropics driving diversification and extinction is a species-area effect. This idea has been proposed before (*36*), but it has received little attention (*37*). During the early and middle Eocene, there was a major global warming event that allowed tropical lineages to expand well into the modern temperate areas (*24*, *25*, *27*). High-diversity forests existed in the early Eocene of northern Patagonia (*12*, *38*), which was located near the southern tip of the tropical belt during the Eocene (*12*). This increase in the area with tropical-like climate could be the main factor enhancing the increase in local diversity in the Neotropics during the Eocene. Larger regions can support more species, which enhance both regional and local diversity (*2*, *35*, *39*) by reducing the risk of extinction and increasing niche opportunities (*2*). In contrast, a cooling event in the late Eocene to early Oligocene reduced tropical areas drastically and, thus, drove local extinction in the Neotropics. A recent analysis of biome

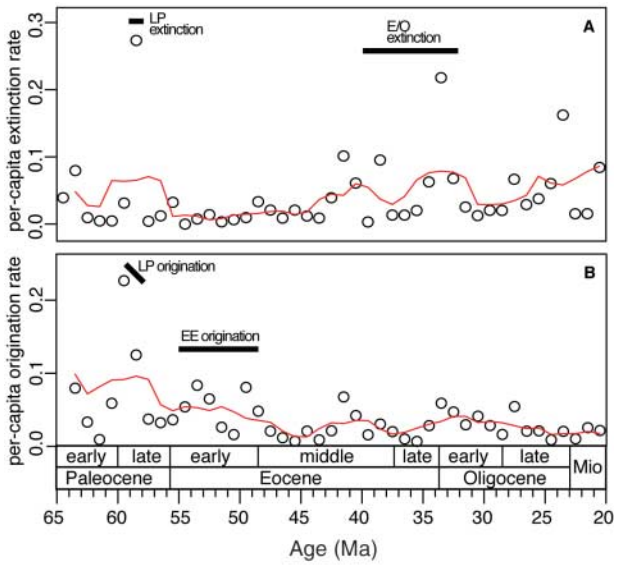

Fig. 3. Per capita rates of origination and extinction (*15*, *20*). (**A**) Per capita extinction rate per million years shows a stable long-term pattern, which increases over background levels during the late Paleocene and the Eocene-Oligocene transition. Raw data were smoothed using a five-point running mean (red line). (**B**) Per-capita origination rate per million years shows a slow, long-term decrease in the rate of origination over time. The rate also increases during the late Paleocene and the early Eocene. Raw data were smoothed using a five-point running mean (red line). LP, late Paleocene; EE, early Eocene; E/O, Eocene-Oligocene.

size integrated over time and diversity also found a primary role for changes in biome area over time in determining current species richness (*37*).

Comparisons with Holocene diversity. Holocene palynological diversity values (Fig. 2A) are lower than early to middle Eocene diversity values, but higher than either Oligocene-Miocene or Paleocene palynofloras (220 to 260 morphospecies). Rarefaction analysis of within-sample diversity also shows the same pattern (*15*). Eocene floras are significantly more diverse than Holocene floras (*t* test, $P < 0.0005$, mean of 44 versus 36 species per sample), and the Early Miocene is less diverse than the Holocene (*t* test, $P < 0.0005$; mean of 30 versus 36 species per sample). This comparison suggests that diversity increased again at some time between the Miocene and the Pleistocene to reach Holocene levels. This increase in diversity could be related to two factors: the 12 to 14 My middle Miocene climate optimum (*27*) that extended tropical areas to midlatitudes or the 5.5 to 3.7 My Andean uplift (*40*, *41*). Although there are now insufficient paleobotanical data to test these two hypotheses, the Andes uplift hypothesis (*40*) seems more likely. There was a long-term cooling phase after the middle Miocene optimum that would have decreased tropical areas and, therefore, would have decreased diversity. On the contrary, the Andes uplift is a more recent event, and a great deal of evidence suggests that it increased speciation: Diversity of Neotropical plants and birds is concentrated along the Andes foothills (*40*, *42*); many Gondwanan families are more speciose near the Andes (*40*); and a radiation of some taxa, such as *Inga,* is inferred as occurring between 10 and 3 My (*43*). High plant-species diversity has also been found to be associated with mountain building, such as the Laramide Front Range during the early Paleocene (*44*). However, a detailed record of Neogene diversity changes in the Neotropics, as the one compiled here for the Paleogene, is needed to test this hypothesis.

The overall pattern shows that plant diversity in the Neotropics has fluctuated greatly through time, as it is sensitive to global temperature. Temperature or precipitation change in the tropics may explain the pattern. An alternative hypothesis involves the control of global climate change on the area available for tropical ecosystems, which could, in turn, affect origination and extinction rates. If the size of forested areas does indeed control levels of local species diversity, conserving isolated pockets of tropical rainforest may not be sufficient to prevent high rates of extinction in the long run.

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Supporting Online Material

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