Paleobiology

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Diversification dynamics of vegetation during the Cenozoic in the Neotropics: a palynological perspective from Colombia

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Article

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Abstract

The Neotropics host the highest diversity of plants on the Earth today and have done since at least the late Paleogene (~58 Ma). Several mechanisms have been proposed to explain this elevated diversity, but the empirical patterns of Neotropical plant diversification that would test key aspects of those mechanisms are still unclear. We use an extensive palynological database from northern South America to characterize patterns of extinction, origination, and diversity and their possible drivers since the Paleogene. The foreland Llanos basin of Colombia preserves the evolutionary history of Neotropical vegetation as well as the geological evolution of northern South America, offering a unique opportunity to study the relationship between the geological and fossil records. The palynological record of the Llanos basin has been intensely studied mainly for oil exploration, and we use this information to infer the evolutionary history of Neotropical vegetation in Colombia during the Cenozoic. There is no straightforward relationship between global temperature and Neotropical plant diversity. Nevertheless, environmental change had an important influence on the dynamics of diversification, especially during volatile climate intervals such as the Paleocene–Eocene and the Pleistocene. Pulses of regional extinction were driven by large-scale temperature excursions, including both warming and cooling phases. Time-lagged origination pulses results in rapid floral replacement on a timescale of 1 Myr. Origination and extinction are essentially balanced on long timescales, leading to a near-zero long-term net diversification rate. Regional geological events, like the uplift of the Andean Cordillera, and changes in paleogeography also played an important role in Neotropical plant diversification.

Non-technical Summary

The Neotropics maintain the highest biodiversity of the planet, exert control in global climate, and play an important role in the dynamics of our planet. Researches from a wide range of disciplines are very interested in understanding how diversity in the Neotropics was produced and how it is maintained through deep time. Despite important advances in our understanding of the origin and diversification of Neotropical biota, we still do not have a clear idea about the patterns of diversification through geological time. This presents a significant knowledge gap that needs to be filled. Fossils are necessary to understand the history of the Neotropical biota. From the perspective of plants, palynology represents the best proxy to study the macroevolution of vegetation. Pollen and spores fossilize readily, they are produced in large amounts and are found in a wide variety of sedimentary environments, and they have high stratigraphic resolution. In this work, we used a compilation of palynological information from Colombia to explore patterns of plant diversification during the Cenozoic and their possible drivers. Changes in global temperature had an important influence on the dynamics of diversification, especially during volatile climate intervals. Paleogeographic changes and regional geological events also had an important role in modeling diversity. Origination and extinction are balanced on long timescales, with pulses of extinction followed by rapid floral replacement on a timescale of 1 Myr. The macroevolutionary history of Neotropical vegetation is a complex puzzle that requires the integration of data from multiple areas of research in biology and earth–physical sciences. The purpose of our work is to provide a small piece of evidence that helps to reconstruct this interesting puzzle.

Introduction

The Neotropics, the geographic region that corresponds to the tropics of the New World (Morrone 2014), host tremendous extant plant diversity and are therefore a model system for understanding the origin and maintenance of biodiversity (Gentry 1992; Perez-Escobar et al.

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2022). Neotropical plant diversity has been attributed to various mechanisms involving both biotic and abiotic factors, including the occurrence of a relatively stable long-term climate regime compared with northern temperate regions, recent diversification events during glacial–interglacial cycles (Haffer 1969), and high origination rates or low extinction rates in the tropics (Stebbins 1974). The Stebbins' (1974) hypothesis poses that the tropics have acted as a "cradle," a "museum," or both, with taxa preferentially originating in the tropics before expanding into higher latitudes (Jablonski et al. 2006), a mechanism that has found strong support from phylogenetic studies of modern flowering plants (angiosperms), which comprise at least 80% of living plant species. Phylogenetic studies of extant angiosperms suggest that per-species origination and extinction rates in the tropics are not substantially different from those outside the tropics. The Neotropics are therefore distinctive among global floristic regions as a macroevolutionary source region that has exported species to other regions thorough most of the Cenozoic (Antonelli et al. 2015).

Although climate is one of the best predictors of species diversity today, its role in producing and maintaining plant diversity in deep time is still under debate. Palynological analysis from the Paleogene of Colombia indicates a correlation between fluctuations in diversity and changes in global temperature (Jaramillo et al. 2006), suggesting that climate variation may be a direct driver of Neotropical plant diversity, possibly by driving variation in available area (Jaramillo et al. 2006). Global warming episodes, such as the Paleocene–Eocene thermal maximum (PETM) and the mid-Miocene climatic optimum (MMCO) are also characterized by short-term increases in origination rates, causing increases in diversity (Jaramillo et al. 2010; D'Apolito 2016). Evidence so far, therefore, suggests that transient climatic warming events promote diversification. Nevertheless, a correlation between diversity and temperature is not very evident on longer timescales. For example, changes in palynological diversity during the Neogene are not closely related to temperature variation (Hoorn and Wesselingh 2010).

A tectonic-related explanation of Neotropical plant diversification has also been proposed (Gentry 1982). The uplift of the northern Andean Cordillera, of which the most intense pulse occurred during the Miocene–Pliocene (Gregory-Wodzicki 2000; Hoorn et al. 2010; Siravo et al. 2019) resulted in substantial changes that affected the paleogeography of northern South America and especially the Amazon Basin (Mora et al. 2010; Rodazz et al. 2010; Leite et al. 2016; Perez-Escobar et al. 2022). This orogenic pulse promoted habitat heterogeneity, created biotic corridors, intensified the nutrient supply, and changed the hydrological and climate regime of the entire continent (Mora et al. 2008; Hoorn and Wesselingh 2010 and references therein). These changes could favor adaptative radiations, produce geographic vicariance, and promote allopatric speciation that may have increased the plant diversity of the region. However, the relationship between orogenic activity of the Andes and long-term patterns of plant diversity has been difficult to prove. The palynological diversity curve proposed by Jaramillo et al. (2006), which is the most complete to date, does not include the Miocene and is restricted to the interval between 66 and 20 Ma. Moreover, it was constructed using range-through methods that are highly prone to distortions such as edge effects (Foote 2000), and more recent methods of diversity estimation (e.g., Alroy 2010a, 2014; Chao and Jost 2012; Chao et al. 2014; Close et al. 2018) have not yet been applied. Other palynological studies in the Amazon basin of Brazil have been restricted to short intervals of the Miocene (Silva-Caminha et al. 2009; D'Apolito 2016; Leite et al. 2016).

Fossils provide unique observations of species in deep time that can shed light on the mechanisms of diversification and are an especially powerful tool for characterizing variation in diversity and rates of diversification and turnover through deep time (Alroy 2000; Foote 2000; Foote and Miller 2006; Silvestro et al. 2019; Flannery-Sutherland et al. 2022). Diversity estimates and measures of taxonomic rates (origination and extinction) have been widely used to study the evolutionary history of organisms, including marine invertebrates (Sepkoski 1996; Foote 1988; Alroy 2008); mammals (Alroy 2009); marine microorganism (Lloyd et al. 2011; Lazarus et al. 2014; Fraass et al. 2015); and tetrapods (Benton 1995; Benson et al. 2016). Although the counts of fossils and the methods used for macroevolutionary estimates can be distorted by factors like sampling bias, the Pull of the Recent, and the Signor-Lipps effect (Raup 1972; Foote and Miller 2006), there is substantial evidence that for a broad perspective on global and regional diversity trends, the methods and compendia of fossils have now matured sufficiently to capture the main biotic transitions preserved in the geological record (Foote and Miller 2006; Alroy 2010a; Quental and Marshal 2010). As a consequence, several approaches and methods to estimate diversity and taxonomic rates from the fossil record are now available (Alroy 2000, 2014; Foote 2000; Foote and Miller 2006; Silvestro et al. 2018, 2019).

The macrofossil record of plants has been successfully used to test macroevolutionary hypotheses. Examples include the origin and diversification of vascular plants (Silvestro et al. 2015), the dispersal and extinction rates across continents during the Cenozoic (Silvestro et al. 2016), the role of biotic and abiotic mechanisms in controlling species diversification in ferns (Lehtonen et al. 2017), and the origin of the modern Neotropical forest (Carvalho et al. 2021).

Microfossils provide another source of information for vegetation dynamics in the geological past, specifically pollen and spores. Due to their role in reproduction, plants tend to produce large amounts of pollen and spores that fossilize readily (Traverse 2007). It has been argued that because pollen and spores lack a sufficient amount of diagnostic synapomorphies that prevent accurate taxonomic classification, they are not a reliable source of information in evolutionary studies of plants (Silvestro et al. 2015). However, it has also been demonstrated that diversity in pollen rain follows the trend of vegetation diversity over ecological gradients (Weng et al. 2006; Birks et al. 2016; Felde et al. 2016. Gosling et al. 2017) and reflects local to regional vegetation conditions well (Gosling et al. 2009; Jantz et al. 2013; Matthias et al. 2015; Julier et al. 2017).

The fossil record of Neotropical macro-plant remains (e.g., leaves, wood, flowers, fruits) is deficient and poorly studied (Wing et al. 2009). Neotropical rock outcrops are scarce and difficult to access due to dense living vegetation. This condition has prevented a complete and continuous fossil record of this region. However, and despite the difficulty of obtaining a good and complete paleobotanical record from the Neotropics, there is one region in Colombia that, due to its importance for oil exploration, has been intensely studied in terms of geology and palynology. This region corresponds to the Llanos basin, a foreland basin that is limited by the Guiana Shield and the Amazon basin to the east and the eastern Andean Cordillera to the west. Due to its geographic position, the Llanos basin preserves a very complete record of the geological and palynological history of the Neotropics (Fig. 1). This basin can therefore be considered to be a natural laboratory to study the relationship between the uplift of the northern Andean Cordillera with its climatic and environmental changes and the macroevolutionary history of Neotropical vegetation during the Cenozoic.

The Llanos basin has been intensely studied in terms of palynology, and an abundant record of fossil pollen and spores from

Figure 1. Map of Colombia showing the geographic location of the sections (wells and outcrops) used in this study. The red circles correspond to the sections used for our estimations of diversity and taxonomic rates. WC, Western Andean Cordillera; CC, Central Andean Cordillera; EC, Eastern Andean Cordillera; CAT, Catatumbo basin.

subsurface drilling/coring can therefore be used to provide insight into the deep-time history of Neotropical plants. In spite of palynology's great potential, only a few studies have used it to approach the evolutionary dynamics of Neotropical vegetation (Hoorn 1993; Jaramillo and Dilcher 2001; Jaramillo et al. 2006; D'Apolito 2016; Leite et al. 2016; Jaramillo 2019). So far, these studies have focused on local geographic areas and were restricted to specific and relatively short intervals of the Cenozoic. This has given us only snapshots of the evolution of Neotropical vegetation and prevented us from attaining a larger understanding of the drivers of Neotropical plant diversity.

Here, we use a high-resolution palynological record obtained from 6098 samples, representing 110 sections (including wells and outcrops) drilled mainly in the Llanos basin of Colombia. We combine the samples to produce a composite section spanning from 66 Ma to the present, estimating diversity and taxonomic rates (origination and extinction) using sampling-standardized methods and evaluating their possible drivers.

Materials and Methods

Composite Section

We analyzed a palynological inventory of 110 sections (Fig. 1; Supplementary Material 1), including both wells and outcrops. Of these, 63 correspond to sites previously analyzed by Jaramillo et al. (2011). Our analysis includes a total of 6098 samples and 2777 morphospecies, of which 1200 morphospecies have informal

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names only. Nevertheless, we are confident about the consistency of morphospecies delimitation, which results from a detailed morphological and taxonomic comparison with species stored in a database hosted by the Biostratigraphy Team of the Instituto Colombiano del Petróleo (ICP-Ecopetrol S.A.), including photomicrographs and morphological descriptions of thousands of palynomorphs found in the Neotropics. All the palynological slides used in this study are stored in the palynological collection of the Ecopetrol Core Library, Instituto Colombiano del Petroleo (ICP), Santander, Colombia.

Samples from all sections were combined in a single composite section using graphic correlation (Shaw 1964; Edwards 1984; Supplementary Material 2). The final composite section includes sediments that accumulated in fluvial to coastal plain environments between the Paleocene and the Holocene (66–0 Ma) (Cooper et al. 1995; Bayona et al. 2007; Parra et al. 2009; Bande et al. 2012; Reyes-Harker et al. 2015). Each part of the composite section includes information from several sections and therefore from different depositional environments and biomes. This approach reduces the chances that differences in environment of deposition influence changes in taxonomic diversity over time. The age of each sample was calculated using the equations of the lines of correlation and the calibration points used by Jaramillo et al. (2011), which include foraminiferal biostratigraphy, stable carbon isotope stratigraphy (δ^{13}C), and key stratigraphic data.

Because most of the material corresponds to ditch-cutting samples, borehole caving can artificially increase the first appearance datum (FAD) of the species, making the apparent time of origination of the species older than the actual time of origination. This could act as a systematic bias in macroevolutionary estimates. To identify the potential influence of caving on the ranges of the species, and therefore on the diversity and taxonomic rates estimates, two versions of the composite section were used. One version (complete version) included all occurrences of all 2777 morphospecies, regardless of the type of samples from which their FADs were interpreted. The other version (restricted version) included only those morphospecies (193) whose FADs have been confirmed using core or outcrop samples. If caving did not substantively affect the ranges of the species, we would expect to find similar results with both datasets, which we do.

Diversity

We used two methods to estimate diversity. First, we estimated standing diversity from our dataset using first appearance data (FADs) and last appearance data (LADs), using a range-through assumption (i.e., assuming that each morphospecies was present at all times through its first and last appearance) (Foote and Miller 2006). This is the approach used by the previous study of large-scale diversity patterns of Neotropical palynomorphs (Jaramillo et al. 2006), but suffers from substantial edge effects (Foote 2000). Indeed, our uncensored, range-through diversity curve and that of Jaramillo et al. (2006) both have a characteristic long-term hump shape consistent with a strong influence of edge effects (Signor and Lipps 1982). Therefore, we also applied a censored version of range-through diversity that makes use of only those species with sampled ranges below a threshold duration. Censorship of the data to include only short-ranged taxa should limit the duration of potential edge effects, rendering the central part of the time series more interpretable and indicates a substantially different diversity pattern (Supplementary Material 3, Supplementary File 1).

Accurate diversity estimates should statistically remove biases imposed by both the counting method and variation in sampling intensity through time. Variation in the quantity of sampling is problematic, because estimated differences in diversity between two samples can be explained by differences in sampling effort and not biological factors. The goal of most resampling methods is to obtain an empirical approximation of a sampling distribution of a statistic of interest and can be used to standardize samples, test statistical hypothesis, estimate standard errors, and carry out other statistical evaluations of empirical datasets (Kowaleski and Novack-Gottshall 2010). In the specific case of diversity estimation, randomized subsampling protocols seek to hold each time interval to a quota of data items. This quota can be expressed in terms of (1) number of taxonomic occurrences; (2) number of fossil collections; and (3) occurrences represented by the collections (Alroy 2010a). Most of the methods to estimate diversity, including classic rarefaction, subsample the data from each interval to attain an entirely uniform and fixed quota of data items (i.e., counts of specimens, counts of occurrences, or counts of fossils collections) (Alroy et al. 2001; Bush et al. 2004). However, uniform-sampling schemes tend to flatten out variation in diversity through time because they are designed to count items, ignoring systematically two prominent features of the fossil record, rarity and commonness (Alroy 2010b). Uniform subsampling is therefore different from fair or representative subsampling. As pointed out by Alroy (2010b), when the actual richness of the species pool is low, it is not necessary to sample very hard, but when richness is high and many taxa are rare, it may be necessary to subsample more intensively to achieve comparable coverage of the species pool. In this case, uniform-sampling schemes fail by undersampling the richer species pool.

Shareholder quorum subsampling (SQS [Alroy 2010a] or “coverage-based rarefaction” [Chao and Jost 2012]) use sampling standardization to estimate richness by subsampling to equal coverage of the species occurrence-frequency distribution. This is intended to achieve fair rather than uniform sample frequencies by tracking not the number of items that are drawn but the coverage of the underlying species pool represented by the species that have been drawn. Coverage is the proportion of the entire frequency distribution represented by the species found so far. The coverage of observed data is modified to estimate the coverage of the real taxon distribution for each sample pool (Alroy 2010a,b). This is achieved by multiplying the coverage of the observed data by Good’s u; the proportion of occurrences representing non-singleton taxa, which is a measure of sample completeness (Alroy 2010a). Standardization in SQS is achieved therefore by drawing enough collections in each time interval to generate the same coverage level. The quorum (q) refers to a certain amount of coverage, if $q = 0.30$ sampling stops when 30% of the distribution is covered. Alroy (2010a,b) proposed that a quorum of 0.4 is the minimum required to recover consistent relative estimates of diversity.

SQS was implemented in three ways using the R package iNext v. 2.0.20 (Hsieh et al. 2016). First, we applied SQS subsampling within individual samples, using the species abundance-frequency distribution (Supplementary File 2). Only samples with counts greater than 50 palynomorphs were included in this analysis as a quality-control threshold. Second, we applied SQS using the pooled species abundance-frequency distributions of all samples within 1 Myr intervals (i.e., using the sum of the abundances reported in all the samples where each species was found) (Supplementary File 3). Third, we subsampled from the species occurrence-frequency distributions, using presence/absence data for species within samples

(Supplementary File 4). In all the approaches, SQS diversity was estimated using a quorum level of 0.6.

The changes in palynological composition were assessed using a constrained hierarchical cluster (Birks and Gordon 1985). The cluster was constructed from the pooled species presence/absence data of all samples within 1 Myr intervals using the range-through assumption after removing singletons. Because each part of the composite section incorporates information from sections deposited in different environments of deposition and biomes, it is difficult to separate the contribution of each biome to the diversity curve. This approach, and the lack of knowledge about the botanical affinity of most of the palynomorphs, prevents an accurate and reliable reconstruction of the geographic distribution of biomes during each time interval. However, the cluster analysis allows us to establish the main differences in the overall plant composition throughout the Cenozoic. For the cluster analysis, we used the package rioja (Juggins 2023; R Core Team 2024).

Taxonomic Rates

By taxonomic rates, we mean the rates at which new morphospecies originate (origination) and existing species become extinct (extinction) (Foote and Miller 2006). A practical impact of estimating origination and extinction rates considering entire age ranges (the range-through assumption) (Foote 2000) is that those metrics introduces a series of biases, such as the Signor-Lipps effect (Signor and Lipps 1982), the Pull of the Recent, and other edge effects, which are difficult to quantify and remove. To correct some of these problems, Alroy (2008, 2010a, 2014) introduced a series of equations (the three-timer equation and the gap-filler equation) to estimate origination and extinction that do not make use of the range-through assumption and instead focus on occurrence data that indicate which taxa are sampled in which time interval. These equations involve examining only a limited sampling window consisting of four consecutive time intervals (i: focal bin; $i-1$, $i+1$, $i+2$). Similar to the approach proposed by Foote (2000), Alroy's method counts the number of taxa sampled in each one of four different categories: two-timers (2T): taxa sampled immediately before ($i-1$) and within focal bin (i); three-timers (3T): taxa sampled in the focal bin (i) and immediately before ($i-1$) and after ($i+1$); part-timers (p): taxa sampled before and after but not in the focal bin; gap-fillers (g): taxa sampled in intervals $i-1$ and $i+2$ but not within interval $i+1$ or in interval $i+2$ and $i+1$, and that may or may not be found in the focal interval. The gap-filler equations work with the four interval-moving windows and consider the categories 2T, 3T, p, and g. Although the gap-filler origination and extinction rate equations use some of the same counts, there is no spurious correlation between them (Alroy 2014). Origination and extinction rates were calculated using the modified versions of the gap-filler equations proposed by Alroy (2015; modified from Alroy 2014) implemented using custom code. Gap-filler rate estimates incorporate an estimate of sampling rate, allowing estimation from incompletely sampled species occurrence data.

Simulations suggest that all methods to estimate taxonomic rates (including boundary-crosser and three-timer and gap-filler equations) might yield different values depending on whether the data are sampling standardized (Alroy 1996; Alroy 2010b). Gap-fillers might produce less noisy values if sampling probabilities are made more uniform. The most employed standardization method is classic rarefaction of taxonomic occurrences (Foote and Miller 2006) and SQS (Alroy 2010a). Because the three-timer and gap-filler methods build in assumptions about the equality of sampling probabilities from one interval to the next, they are better met by data that are previously standardized using classic rarefaction (Alroy 2014). In our work, the taxonomic rates using the gap-filler method are based on classic rarified data.

We divided the complete composite section into 1 Myr time intervals (bins) and standardized by randomly drawing entire collections up to a uniform quota of 85 samples per bin. Resampling was repeated 1000 times, and origination and extinction were calculated for each one of the iterations. The median origination and extinction rates were calculated from 1000 subsampling iterations (Supplementary Files 5, 6). We calculated diversification rates as being origination rate minus the extinction rate. We calculated turnover rates as the smallest value of either origination or extinction rate within each time interval. This is an index of the proportion of species that became extinct and were quantitatively replaced by new species within each interval.

Results

Diversity

The analyses of the two versions of the composite section yield similar diversity estimates using equal coverage subsampling (SQS; Alroy 2010a; Chao and Jost 2012; Supplementary Material 4, - Supplementary Fig. 2). This indicates that any potential effect of borehole caving on diversity estimation is almost undetectable. Our interpretation therefore focuses on the complete composite section, which incorporates information from a much greater number of species (2777 species, compared with 193 in the restricted composite section). The abundance-based, per-sample analysis yields a cloud of points in which each point represents one sample (Supplementary Material 5, Supplementary Fig. 1). Variation in sampling intensity through the Cenozoic is clearly evident, with relatively sparse sampling during the early-middle Eocene and late Miocene–Pleistocene. This analysis also demonstrates substantial variation in diversity among samples of the same interval through the Cenozoic (Supplementary Material 5).

Diversity curves based on SQS of occurrence data agree with the values obtained from abundance data (Supplementary Mate rial 5, Supplementary Fig. 3) regarding the most prominent patterns. However, in the occurrence version, the sampled coverage of the underlying taxon pool is insufficient for several bins of the Eocene and Miocene and does not provide information of diversity. We used a quorum level of 0.6, because at this quota it was possible to obtain SQS diversity estimates for all the bins. Is important to note that different quorum levels reproduce very well the most prominent changes in diversity (Supplementary Material 5, Supplementary Fig. 4).

Our curve exhibits three broad phases of diversity (Fig. 2). Diversity during the early Cenozoic (Paleocene–Eocene) shows high-amplitude short-term fluctuations, whereas later Cenozoic diversity estimates (Oligocene–Miocene) were more stable on short timescales, followed by a return to fluctuating diversity estimates in the past 5 Myr (Pliocene–Recent) (Fig. 2). SQS diversity does not correlate with $\delta^{18}O$ using the complete dataset (66–0 Ma) or when they are analyzed separately (66–34.5 Ma and 33.5–0.5 Ma) (Table 1). The overall shape of our curve differs markedly from a previous standing diversity curve obtained using range-through taxon counts (Jaramillo et al. 2006). We attempted to mitigate these edge effects by limiting analysis to only those taxa with relatively short ranges, spanning less than 70 Myr, 20 Myr, and less than 10 Myr. The resulting diversity curves (Supplementary Material 3)

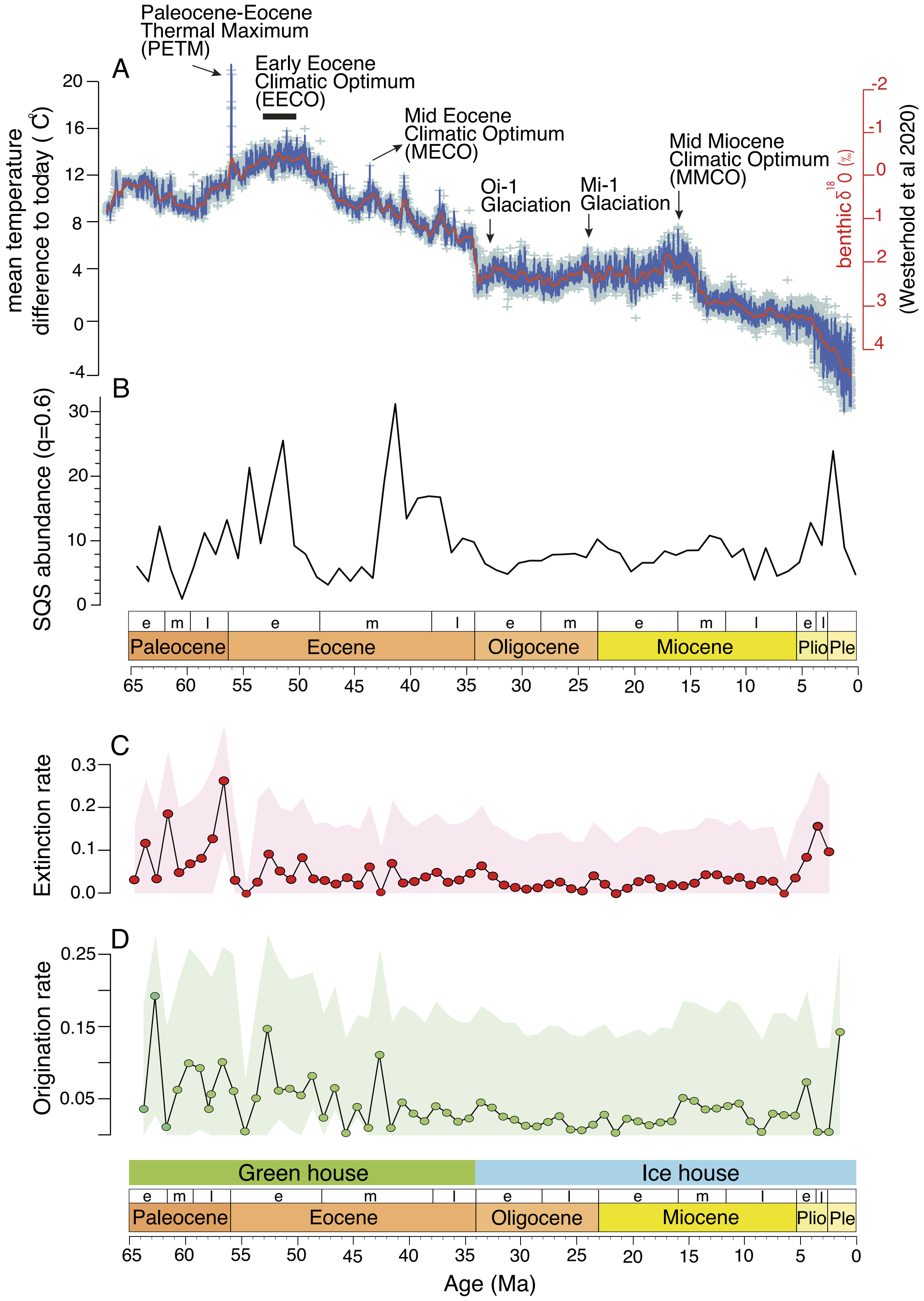

Figure 2. Changes in palynological diversity and taxonomic rates during the Cenozoic. **A,** Cenozoic oxygen isotope record for benthic foraminifera showing the most prominent global climate change events during the Cenozoic (modified from Westerhold et al. 2020). **B,** Pollen and spore diversity estimated using abundance-based shareholder quorum subsampling (SQS) at a quorum (*q*) of 0.6. **C,** Extinction rates estimated using the gap-filler equation (Alroy 2010a, 2014). Extinction shows an increasing trend during the Paleocene, short-amplitude fluctuations during the Eocene to middle late Miocene interval, and an increasing trend during the late Miocene to Pleistocene. **D,** Origination rates estimated using the gap-filler equation (Alroy 2010a, 2014). Origination exhibits wide amplitude fluctuations during the Paleocene to middle Eocene, with at least three outstanding peaks occurring during the early Paleocene and early and middle Eocene. From the middle Eocene to the late Miocene, the origination rates exhibit short-amplitude fluctuations without apparent peaks. The Pleistocene is characterized by an abrupt increase in origination. The shaded area in extinction and origination rates indicates 95% confidence intervals derived from iterations of the sampling-standardization procedure.

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Table 1. Spearman's rank correlations between shareholder quorum subsampling (SQS) diversity (quorum 0.6) and the δ^{18}O global climatic proxy. Detrending was carried out using first differences.

Start interval	End interval	Treatment	*N* (intervals)	Coefficient (occurrences)	*p*-value	Coefficient (abundances)	*p*-value
Paleocene	Recent		66	−0.347	0.005*	−0.283	0.022*
Paleocene	Recent	Detrended	65	0.036	0.778	0.148	0.241
Paleocene	Eocene	Greenhouse	32	0.026	0.886	0.181	0.319
Oligocene	Pleistocene	Icehouse	29	0.19	0.322	0.126	0.525

*Significant.

mimic some, but not all, features of our SQS diversity curves, including high diversity during the mid-late Eocene and relatively low, stable diversity since then.

Diversity increased during the Paleocene–early Eocene, from initially low levels associated to the effects of the K-Pg boundary extinction event. Short-lived peaks of high diversity approximately coincide with global warming events of the PETM and the early Eocene climatic optimum (EECO) (Fig. 2). Low diversity values during the middle Eocene were followed by a peak coinciding with the mid-Eocene climatic optimum (MECO) at ~42.5 Ma. Diversity then decreased until the end of the Eocene and remained low during the Oligocene and early Miocene (Fig. 2). The early Oligocene Oi-1 glaciation (~33.7 Ma) coincided with low diversity, whereas the late Oligocene Mi-1 glaciation (~24 Ma) coincided with transient, higher diversity before diversity decreased during the final 3 Myr of the Oligocene. A pattern of increasing diversity through the Miocene culminated in relatively high diversity after the MMCO (15–17 Ma) before decreasing to lower levels in the late Miocene (Fig. 2). Diversity was relatively high during the Pliocene and Pleistocene, with peaks during the early Pliocene and early Pleistocene (Fig. 2).

The constrained stratigraphic cluster shows two main groups, Paleocene–Eocene cluster (PE) and Oligocene–Miocene–Plio-Pleistocene cluster (OMP), which in turn are divided into smaller groups (Fig. 3). The PE and OMP clusters separate two different palynofloras. The PE cluster includes samples from the Paleocene and the Eocene, while the OMP includes samples from the Oligocene, Miocene, Pliocene, and Pleistocene (Fig. 3). The PE cluster is subdivided into two groups. The first group includes samples exclusively from the Paleocene, while the second group divides the Eocene into two groups (Fig. 3). The OMP cluster is also subdivided into two groups. The first group includes samples from the Oligocene and the early-middle Miocene, while the second group encompasses samples from the late Miocene, Pliocene, and Pleistocene (Fig. 3).

Taxonomic Rates

Origination and extinction rates show a pattern of high volatility during the Paleocene–Eocene, with variation in extinction rates being especially high during the Paleocene, and variation in origination being remaining high throughout the Paleocene–Eocene. This was followed by stability at low values for most of the Oligocene–Miocene, and an increase to higher volatility during the Pliocene–Pleistocene (Fig. 2). Variation in extinction and origination rates is broadly congruent with patterns of relatively volatility in the SQS diversity curve, although it does not result from estimation from the same underlying data: origination and extinction rates were estimated using a subsample moving window method, based only on the patterns of presence/absence of taxa within four

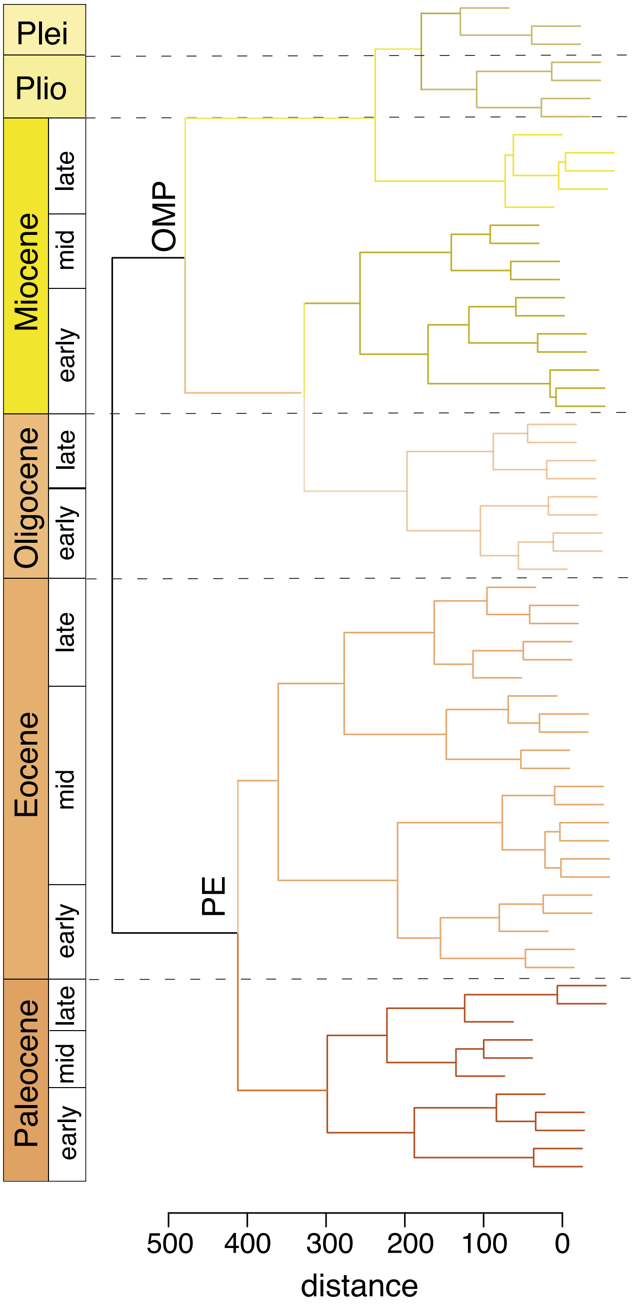

Figure 3. Constrained stratigraphic cluster showing differences in plant composition through the Cenozoic. Two main groups, Paleocene–Eocene cluster (PE) and Oligocene–Miocene–Plio-Pleistocene cluster (OMP), separate the Paleocene and Eocene from the Oligocene, Miocene, Pliocene, and Pleistocene.

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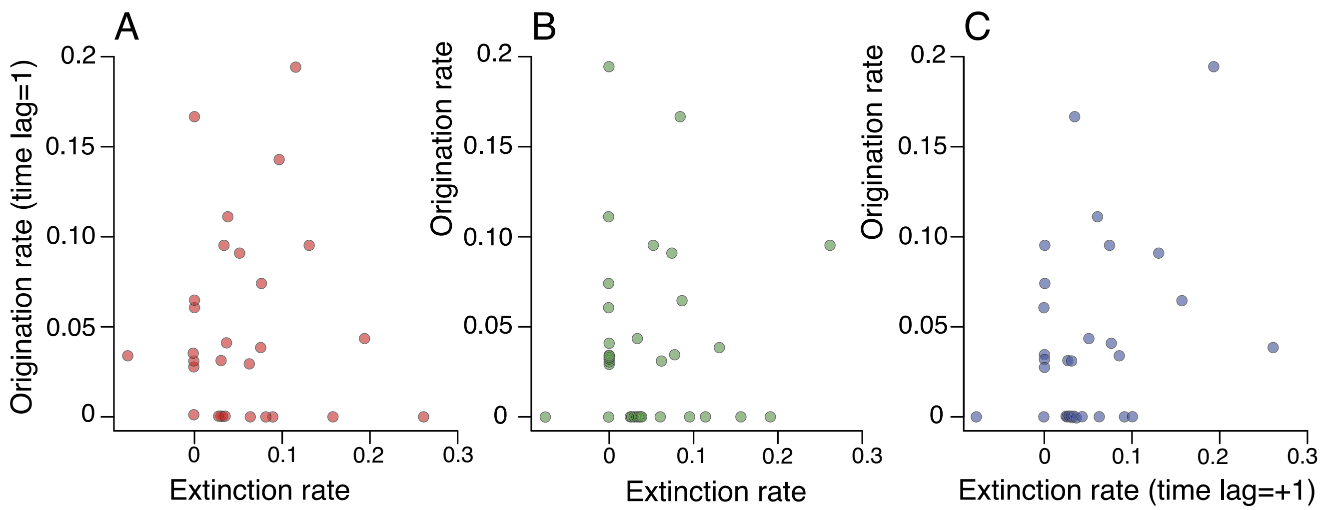

Figure 4. Extinction vs. origination rates. Correlation is maximized at a time lag of one interval (Table 2). **A,** Extinction rate lags origination rate; **B,** extinction rate vs. origination rate; **C,** extinction preceded origination.

consecutive time bins (Alroy 2015), whereas SQS diversity is estimated only from patterns of relative abundance within each time bin (Alroy 2010a; Chao and Jost 2012). Peaks of elevated extinction are evident during the early Paleocene (64–63 and 62–61 Ma), the Paleocene/Eocene transition (57–56 Ma), and during the Pliocene (5–2 Ma), with smaller peaks evident at other time intervals (e.g., 53–52 Ma, 50–49 Ma, 42–41 Ma), including the Eocene/Oligocene transition (34–33Ma) (Fig. 2). Peaks of elevated origination are evident during the early Paleocene (63–62 Ma), the EECO (53–52 Ma), MECO (43–42 Ma), Pliocene and Pleistocene (5–0 Ma), with smaller peaks frequently evident in the Paleocene and early to mid-Eocene, as well as during the Eocene/Oligocene transition (34–33 Ma) and middle Miocene (Fig. 2). The correlation between extinction and origination rates is maximized at a time lag of one interval (Fig. 4, Table 2), indicating that regional extinctions are generally followed by origination, with a delay of approximately 1 Myr (Table 2). Comparison between origination and extinction for a time lag of zero is significant in only 9.3% of iterations of our sampling-standardization procedure (Table 2).

Diversification rates also show their highest volatility in the Paleocene–middle Eocene and Pliocene–Pleistocene, with especially high relatively stability during the Oligocene (Fig. 5). A period of high-amplitude fluctuations of both diversification and turnover rates is concentrated in the Paleocene and Eocene, marked by high positive diversification rates at 63–62 Ma and 43–42 Ma, and high negative diversification rates at 62–61 Ma and 57–56 Ma, immediately before the Paleocene/Eocene boundary and during the Pliocene (5–2 Ma). Large positive diversification shifts do not generally coincide with high turnover. However, large negative diversification shifts often do, as seen around the Paleocene/Eocene boundary and during the early-late Pliocene transition. High turnover also occurs at 53–52 Ma, around the onset of the EECO and associated with only a weak positive diversification (Fig. 5).

Diversification and turnover show low to null variability during the Oligocene and Miocene, interrupted by relatively higher levels of turnover at the Eocene/Oligocene boundary and in the middle Miocene, possibly related to the MMCO (Fig. 5). A noticeable difference occurs in the Oligocene, where the turnover rate exhibits low-amplitude fluctuations, while the diversification rate is approximately zero during this interval (Fig. 5).

Taxonomic Rates versus Climate

We compare our diversity and taxonomic rate estimates with the climatic curve proposed by Westerhold et al. (2020), which indexes global climate rather than regional temperature variation. However, there is no obvious reason why this disconnect of scale could cause false-positive correlations, and it therefore provides a conservative test of the potential effects of temperature variation on Neotropical plant diversification. Temperature change from one interval to the next is not correlated with either origination or extinction rates. However, stronger correlations are obtained when considering the positivized net temperature change over longer intervals, maximizing at 3 Ma, for which the correlation with extinction rates is positive and significant (Table 3, Fig. 6). This effect is especially evident during the middle Paleocene cooling (up to 61 Ma), warming up to the Paleocene–Eocene boundary (56 Ma), and Pleistocene cooling (up to 3–2 Ma) (Fig. 6). A less prominent effect is also evident at the Eocene/Oligocene boundary (33.9 Ma).

Discussion

Our diversity curve reveals differential dynamics of climate and vegetation during greenhouse and icehouse intervals. Greenhouse

Table 2. Summary of Spearman's rank-correlation test results between origination rates and extinction rates at a lag time. Results are summarized across 1000 iterations subsampling to a uniform quota of 85 occurrences within each 1 Myr interval

Extinction bin	Origination bin	Correlation coefficient (median)	*p*-value (mean)	Proportion significant ($p < 0.05$)
i – 1	*i*	–0.142	0.261	0.192
i – 1	*i*	0.287	0.050*	0.635
i	*i*	0.05	0.44	0.093
i + 1	*i*	0.01	0.498	0.055
i + 2	*i*	0.191	0.144	0

*Significant.

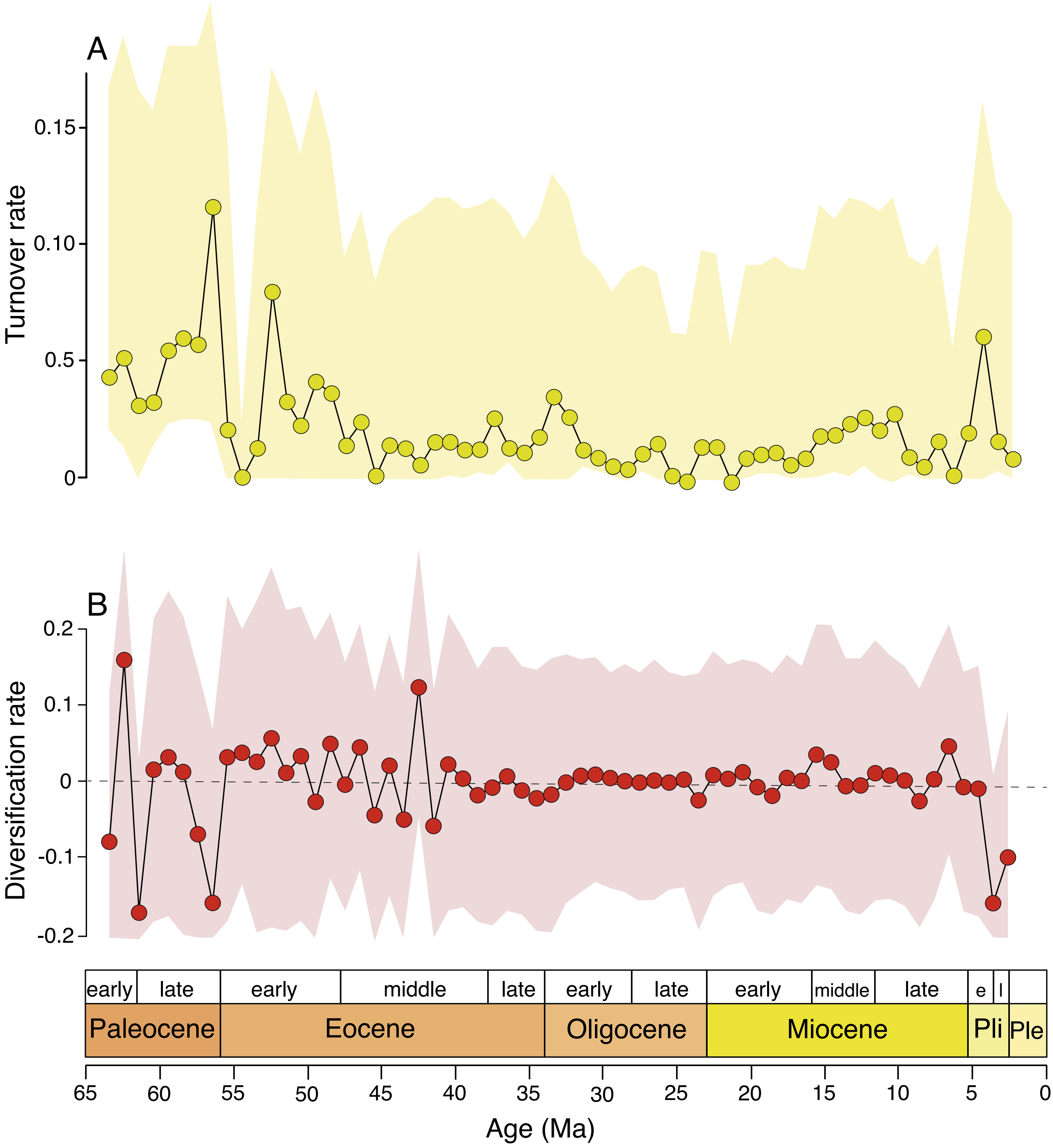

Figure 5. Changes in turnover and diversification rates during the Cenozoic. **A**, Turnover rates (origination rate + extinction rate) show high volatility during the Paleocene to early Eocene. **B,** Diversification rates (origination rate – extinction rate) exhibit high volatility in the Paleocene–middle Eocene and Pliocene–Pleistocene intervals and stability during the Oligocene. The shaded area indicates 95% confidence intervals derived from iterations of our sampling-standardization procedure.

conditions of the Paleocene–Eocene were globally warmer than today, with minimal or no glaciation and lacking polar ice caps (Huber and Thomas 2009), and show volatile patterns of diversity and diversification (Fig. 2). In contrast, icehouse conditions commenced during the middle Eocene to early Oligocene with global cooling and the onset of Southern Hemisphere glaciation and expanded during the late Miocene–early Pliocene with further cooling and the onset of Northern Hemisphere glaciation. This long interval showed relatively greater climate stability, and we find also more stable patterns of diversity and diversification (Figs. 2, 5). The cluster analysis also reveals significant differences in terms of plant composition between the greenhouse and icehouse intervals. The two most relevant groups (PE and OMP) clearly separate samples of the Paleocene and Eocene from samples of the Oligocene, Miocene, Pliocene, and Pleistocene (Fig. 3). The change from greenhouse to icehouse conditions was accompanied by a change in

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Table 3. Spearman's rank-correlation test results between net temperature change over multi-million-year intervals and taxonomic rates at a lag time.

Temperature change interval (Ma)	Directional or positivized	Correlation coefficient (extinction)	*p*-value	Correlation coefficient (origination)	*p*-value
1	Directional	0.04	0.754	0.02	0.878
2	Directional	0.234	0.067	–0.036	0.78
3	Directional	0.178	0.169	0.016	0.902
4	Directional	0.128	0.327	–0.045	0.73
1	Positivized	0.013	0.921	–0.011	0.932
2	Positivized	0.233	0.068	0.009	0.942
3	Positivized	0.272	0.034*	0.22	0.083
4	Positivized	0.182	0.164	0.196	0.129

*Significant.

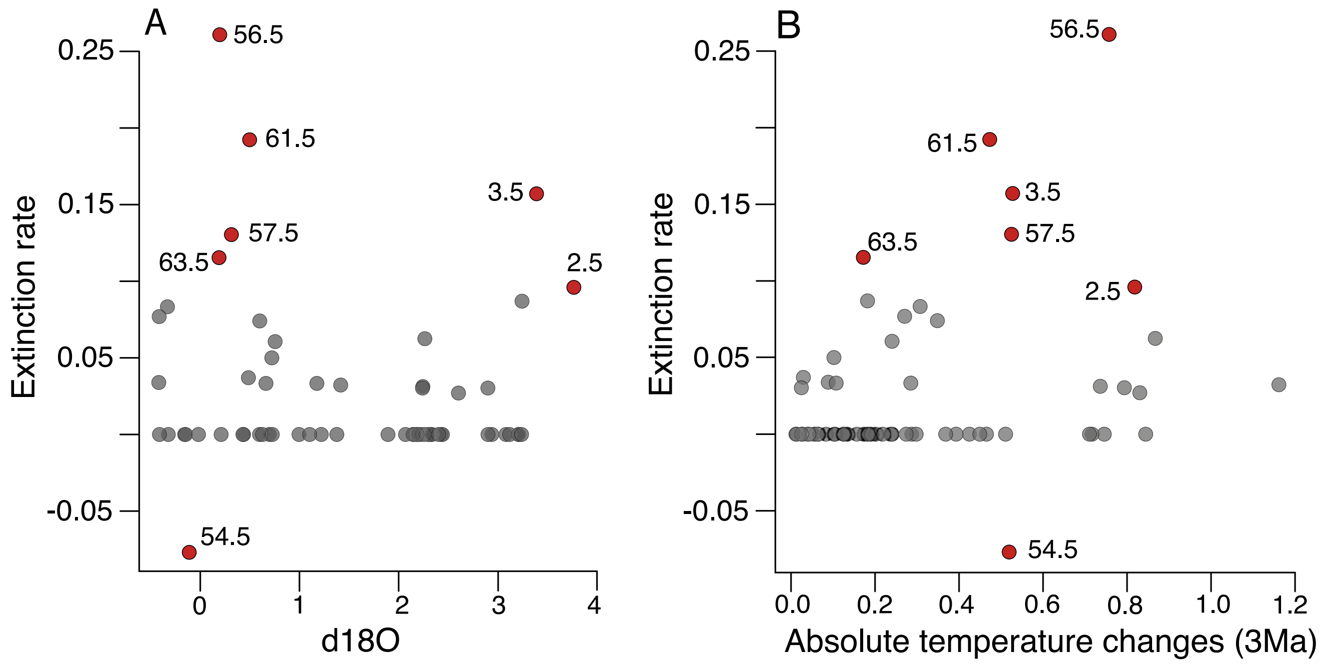

Figure 6 Temperature vs. extinction rates. **A**, Correlation between temperature change between one interval to the next and extinction rates estimated using the gap-filler equation (Alroy 2010a, 2014); **B,** strong, positive, and significant correlation between extinction rate and temperature change over long intervals of time (e.g., 3 Myr).

plant composition that is reflected in the diversity and taxonomic estimates.

The diversity curve also reveals an early increasing trend during the Paleocene–Eocene greenhouse interval, culminating in high diversity by the early Eocene. Regional extinction and origination rates are elevated and highly fluctuating during this interval (Fig. 2). The relatively low palynological diversity and high volatility of the extinction and origination rates during the Paleocene may be a direct consequence of the effect that the K-Pg transition had on tropical vegetation, potentially reflecting long-term ecosystem instability in the wake of this mass extinction event. This resulted in dramatic differences in palynological composition between the Cretaceous and the Paleocene (de la Parra et al. 2022). Plant extinctions levels over the K-Pg boundary were high in the Neotropics, causing low diversity levels for at least 6 Myr after the extinction event (Carvalho et al. 2021), as reflected in our diversity curve (Fig. 2).

The increasing trend in diversity is punctuated by two outstanding peaks that show a good correspondence with global warming events of the PETM and the EECO (Fig. 2). The PETM is recognized as a rapid (<20 ka) worldwide warming event that was possibly driven by the destabilization of carbon from surface sedimentary reservoirs such as methane hydrates (Dickens et al. 1995) or by the volcanisms associated with the North Atlantic Igneous Province (Gutjahr et al. 2017). In northern South America, palynological studies reveal a rapid and distinct increase in plant diversity and origination rates through the PETM (Rull 1999; Jaramillo and Dilcher 2000). Because most of the species in the Eocene have been reported consistently only in South America, the increase in diversity in the Eocene was mainly driven by in situ origination rather than by immigration from other latitudes (Jaramillo et al., 2010). Our diversity curve confirms the results of Rull (1999), Jaramillo and Dilcher (2000), and Jaramillo et al. (2010) in the sense that the Paleocene exhibits lower diversity than the early Eocene (Fig. 2).

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The EECO is the culmination of a long period of global warming and represents the highest ocean temperatures of the last 66 Myr (Miller et al. 1987). An increase in plant diversity has been documented in both southern and northern middle to high latitudes (Christophel 1995; Wing et al. 1995). In the Neotropics, no palynological work has specifically focused on this interval. Our diversity curve shows an outstanding peak at the EECO, which is in fact the second most prominent of the Cenozoic (Fig. 2). Although, the global warming during the EECO could explain the increase in diversity, it is also possible that changes in the paleogeography have played an important role in controlling diversity. The paleogeographic reconstructions by Reyes-Harker et al. (2015) suggest an increase of the area of active deposition between the late Paleocene and the early-middle Eocene. A change from coastal plain and fluvial environments during the late Paleocene to exclusively fluvial environments during the early-middle Eocene is also evident (Reyes-Harker et al. 2015). An increase of the geographic area has been cited as an important factor that can boost diversity via the area–species relationship (Rosenzweig 1995). This relationship proposes that larger regions can support more species, which enhance both regional and local diversity by reducing the risk of extinction and increasing niche opportunities (Fine et al. 2011). The predominance of fluvial environments during the early-middle Eocene may have created geographic barriers that promoted diversification through allopatric speciation.

Using the SQS method, we also find evidence for an interval of relatively low plant diversity during the early-middle Eocene, spanning approximately 50–43 Ma, and potentially related to abrupt temperature decreases following the EECO (Fig. 2). In contrast, according to the boundary-crosser diversity estimates using RTM (Supplementary Material 3, Supplementary Fig. 1; see also Jaramillo et al. 2006), diversity remained high during this interval. This discrepancy suggests that taxa that were extirpated from the study region during this interval were not globally extinct, but underwent range shifts resulting in temporary absence or reduction of their abundance, which makes them difficult to detect. This finding, and our broader finding of high volatility of regional extinction and origination during the Paleocene–Eocene, may be consistent with studies using large phylogenies of extant plant species, which find that the Paleocene and Eocene correspond to the periods of the Cenozoic with the highest rates of emigration from the Neotropics (Romero 1993; Wilf et al. 2005; Antonelli et al. 2015). Our findings suggest, therefore, that a shift in the species range out of the Neotropics during the early Eocene was triggered and facilitated by the geographic expansion of the Neotropics during the EECO (Jaramillo and Cárdenas 2013) and the apparent absence of significant physical barriers such as marine corridors or lacustrine systems (Reyes-Harker et al. 2015).

At the Eocene/Oligocene boundary, the planet changed from a warm ice-free greenhouse world to a glacial Antarctic icehouse world (Francis et al. 2008; Westerhold et al. 2020). This transition exhibits a prominent decrease in diversity, which is evident from the upper segment of the middle Eocene, alongside somewhat elevated turnover rates induced by locally high extinction and origination rates (Fig. 5). The declining trend of diversity shows a good correspondence with the cooling trend suggested by the oxygen isotopic curve (Fig. 2). Analysis based on palynology and macrofossils indicates an increase in seasonality in the middle to late Eocene, which changed the plant composition and allowed the establishment of a tropical dry forest (Martínez et al. 2021). Our cluster analysis seems to corroborate the change in plant composition between the middle and late Eocene (Fig. 3). The onset of a different type of ecosystem should increase ecological heterogeneity and species diversity at regional scale, unless all regional ecosystems are fully replaced by this low-diversity ecosystem. However, the geographic distribution of this new type of ecosystem is still unclear. The work by Martínez et al (2021) is based on a single locality in the Middle Magdalena Valley of Colombia, and to our knowledge there are no data to test whether a tropical dry forest was also present in the Llanos basin at that time. If the establishment of the tropical dry forest was a geographically restricted event, we hypothesize that the declining trend in diversity during the middle Eocene to Oligocene was mainly controlled by the cooling of the planet.

Fluctuations in global temperature during the Oligocene to Pliocene were lower in amplitude than those during the Paleocene to Eocene (Fig. 2). In the Neotropics, this change was accompanied by important regional events like the increase of the orogenic activity in the Andean Cordillera (Mora et al. 2010, 2020), the onset of the Amazon River (Hoorn et al. 2017), and the occurrence of regional marine flooding events (Hoorn et al. 2010; Reyes-Harker et al. 2015; Jaramillo et al. 2017; de la Parra et al. 2019). Our results suggest that for diversity, and especially for origination, extinction, and diversification, the Oligocene–Pliocene interval shows relatively less variation than other intervals (e.g., Paleocene to middle Eocene), lacking major extinction pulses but with notable episodes of turnover during the middle Miocene and the Pliocene.

The most intense peaks of orogenic activity in the north of the Andean Cordillera occurred during the middle Miocene to early Pliocene (12.4–4.4 Ma) (Hoorn et al. 2010; Mora et al. 2010), which also show a declining trend in global temperature starting at the end of the MMCO and ending in the early Pliocene (Fig. 2). Our diversity curve shows a declining trend from the end of the middle Miocene to the late Miocene and two outstanding peaks in the Pliocene and Pleistocene that are accompanied by relatively elevated volatility in the extinction and origination rates (Fig. 2). It is well established that the intense pulse of orogenic activity during the Miocene–Pliocene promoted allopatric speciation that may have increased the plant diversity in the region. The process of diversification does not exclusively correspond to in situ diversification, but immigrant lineages from both the north (Sklenář et al. 2011) and south (Bacon et al. 2018) played an important role in the historic assembly of the Neotropical flora (Hoorn and Wesselingh 2010). The recent and rapid diversification of the Andes lineages could be explained by massive increase in the area of suitable habitats and opportunities for allopatric speciation, as a consequence of the Andean uplift and late Neogene climate changes (Mora et al. 2008; Bacon et al. 2018).

The increase in diversity since the late Miocene would reflect diversification in the highlands rather than in the lowlands. Our diversity curve captures this diversification, because the composite section integrates information from different sites and therefore from different biomes. It is very likely that this process began in the late Miocene, because the cluster analysis shows that the late Miocene is more similar, in terms of plant composition, to the Pliocene and Pleistocene than to the early or middle Miocene (Fig. 3). The low diversity detected during the middle to late Miocene (Fig. 2) may be the result of a bias in preservation produced by the reconfiguration of the drainage pattern. The influx of sediments from the Andean Cordillera produced alluvial deposits and scarce fine-grained deposits, which are those preserving palynomorphs. In fact, the Guayabo Formation and its lithostratigraphic equivalents (middle to late Miocene) correspond to coarse-grain sandstones, conglomerates, and sporadic claystones deposited in fluvial–alluvial to deltaic environments (Bayona et al. 2008) in which it is very difficult to recover palynomorphs.

Our analyses have broad implications for understanding interactions between climate and regional extinction and origination. Extinction rates are correlated with directional long-term climate excursions on a timescale of 3 Myr. Origination rates are correlated with extinction in the preceding interval at a timescale of 1 Myr, but the reverse is not true (Table 1). This suggests that global climate state changes have a strong influence on regional extinction and that intervals showing elevated extinction rates are followed by intervals of high origination rates, resulting in an overall pattern of climate-induced turnover. Punctuated climatic events like the EECO, MECO, Oi-1, and MMCO show good correspondence with elevated turnover rates (Fig. 2). These results agree with the idea that the Neotropics have acted as an engine for global plant diversity, with species being formed and replacing each other at unparalleled rates (Antonelli et al. 2015). This engine seems to have run at higher power during the Paleocene and Eocene, and also during the Pliocene. In this sense, the dynamics of Neotropical vegetation during the Cenozoic are comparable to fern dynamics diversity, which is primarily driven by environmentally induced extinctions, with origination being an opportunistic response to diminishing ecospace occupancy (Lehtonen et al. 2017).

Our results shows that there is no straightforward relationship between temperature and Neotropical plant diversity, but climate shifts seem to have had important effects on the dynamics of diversification, with large temperature excursions causing elevated extinction rates. This acts as a mechanism of turnover, because origination is caused by extinction on a timescale of approximately 1 Myr. However, net diversification is approximately zero on intermediate timescales, so the association of standing diversity with climate variation is more complex than a simple association of high temperature with high diversity. Paleogeography also played an important role in controlling plant diversity. The uplift of the Andean Cordillera, the changes in the area of active deposition, and the evolution of the landscape promoted diversification. However, the most relevant paleogeographic changes show a close correspondence with global climate events. Hence, it is difficult to separate the effects of each one, and it is possible that a combination of climate and paleogeography are responsible for modeling plant diversification during the Cenozoic in the Neotropics.

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