

## 140 Million Years of Tropical Biome Evolution

<https://doi.org/10.32685/pub.esp.36.2019.06>

Published online 3 October 2019

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**Abstract** The origin and development of Neotropical biomes are central to our understanding of extant ecosystems and our ability to predict their future. During the Cretaceous, biomass of tropical rainforests was mostly dominated by gymnosperms and ferns, forest structure was poorly stratified and the canopy was open and dominated by gymnosperms. Extant tropical rainforests first developed at the onset of the Cenozoic, as a result of the massive extinction of the Cretaceous – Paleocene boundary. Paleocene rainforests were multistratified, with an angiosperm-dominated canopy that had high photosynthetic potential. Tropical climate has followed global patterns of warmings and coolings during the last 60 Ma. Rainforest diversity has increased during the warmings while it has decreased during coolings. Several extant biomes, including páramos, cloud forest, savannas, and dry/xerophytic forest, have increase significantly during the late Neogene at the expense of the reduction of the rainforest. Timing and drivers of these changes are still unknown but seem to be related to the onset of our modern, cool-state climate since the onset of the Pleistocene, 2.6 Ma ago.

**Keywords:** *Neotropical biomes, tropical rainforest, gymnosperms, angiosperms, evolution.*

**Resumen** El origen y el desarrollo de los biomas neotropicales son fundamentales para nuestra comprensión de los ecosistemas actuales y nuestra capacidad para predecir su futuro. Durante el Cretácico, la biomasa de los bosques tropicales estaba dominada principalmente por gimnospermas y helechos, la estructura del bosque no poseía una estratificación marcada y el dosel era abierto y dominado por gimnospermas. Los bosques tropicales actuales se desarrollaron por primera vez al inicio del Cenozoico, como resultado de la extinción masiva del límite Cretácico–Paleoceno. Los bosques tropicales del Paleoceno eran multiestratificados, con un dosel dominado por angiospermas con alto potencial fotosintético. El clima tropical ha seguido patrones globales de calentamiento y enfriamiento durante los últimos 60 Ma. La diversidad del bosque tropical ha aumentado durante los calentamientos y disminuido durante los enfriamientos. Varios biomas que hoy existen, incluyendo páramos, bosques nubosos, sabanas y bosques secos/xerofíticos, han crecido significativamente desde el Neógeno tardío en áreas ocupadas previamente por el bosque tropical. Las causas y temporalidad de este cambio masivo en el paisaje aún se desconocen, pero parecen estar relacionadas con el inicio de nuestro clima frío moderno desde el comienzo del Pleistoceno, hace 2,6 Ma.

**Palabras clave:** *biomas neotropicales, bosque tropical, gimnospermas, angiospermas, evolución.*

*Citation:* Jaramillo, C. 2019. 140 million years of tropical biome evolution. In: Gómez, J. & Píñilla-Pachon, A.O. (editors), *The Geology of Colombia, Volume 2 Mesozoic. Servicio Geológico Colombiano, Publicaciones Geológicas Especiales 36*, p. 209–236. Bogotá. <https://doi.org/10.32685/pub.esp.36.2019.06>

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## 1. Introduction

The biota that occupies tropical landscapes is anything but stable. Over geological time, forests have transformed into deserts and vice versa. Entire mountain chains are created while others are weathered away. What are the main drivers of tropical landscape change? How do geology and climate interact with each other to transform plant and animal communities? And how does the biota, in turn, affect its landscape, the climate, and ultimately our survival?

We are studying a number of dramatic landscape changes that have occurred in the tropics over the past 140 million years and how they have influenced the extinction and origination of tropical biotas: From the extreme effects of global warming during the early Cenozoic 50 million years ago to the global cooling of the Pleistocene 2.6 million years ago; from the lifting of the Andes mountains to the creation of savannas; from periods with low levels of CO<sub>2</sub> to events with extremely high CO<sub>2</sub>, similar to the levels that we will reach by the end of the century.

The most extensive biome within the Neotropics is the lowland tropical rainforest. It has the largest number of plant species on Earth, about 90 000, most of them (~96%) angiosperms (Thomas, 1999). Many hypotheses have been proposed to explain why it is so diverse, how it originated, and how its diversity is maintained (Connell, 1971; Fine & Ree, 2006; Gaston, 2000; Gillett, 1962; Hoorn et al., 2010; Jablonski, 1993; Janzen, 1970; Kreft & Jetz, 2007; Leigh et al., 2004; Leighton, 2005; Moritz et al., 2000); these are well summarized by Leigh et al., 2004. There are hypotheses that consider the key factor to be the low rates of extinction and/or high rates of origination in the tropics over millions of years while other consider the high diversity to be developed during the last 2.6 Ma during the Quaternary period driven by habitat fragmentation (Haffer, 1969). The problem to solve is not only how the tropics generate more species than other regions but also how that diversity is maintained (Leigh et al., 2004). Moreover, not only do tropical forests have high diversity, but they also have a unique, multistratified forest structure. When did this structure originate? What were its effects, if any, on the water cycle, nutrients, and carbon at a local, regional, or global level? (Boyce & Lee, 2010; Burnham & Graham, 1999; Burnham & Johnson, 2004). Such questions have puzzled scientists for more than a century but still remain unanswered, yet they are critical to understanding how tropical biomes will respond to our ongoing climate change.

Extant Neotropical rainforests are dominated mostly by angiosperms (flowering plants). A natural starting point to unravel the evolution of extant biomes, therefore, is the time of angiosperm origination, which occurred during the Early Cretaceous, ca. 145 Ma ago (Sun et al., 2002). The history of extant Neotropical biomes comprises a total transformation of how the landscape is occupied, from a forest with no angiosperms at the

onset of the Cretaceous to the extant forest fully dominated by them. This change is far more substantial than for temperate forests, many of which are still dominated by gymnosperms as they were at the onset of the Cretaceous.

There always have been forests in tropical latitudes, therefore, it is important to define what I mean by a Neotropical rainforest, as this term has various meanings. Here I follow the definition of Burnham & Johnson (2004) and Jaramillo & Cárdenas (2013), which refers to a forest defined by the combination of four parameters: climate, floristic composition, vegetation structure, and plant physiognomy. Accordingly, a Neotropical rainforest is a lowland forest, with high mean annual precipitation (>1.8 m/y), high mean annual temperature (>18 °C), low temperature seasonality (< 7 °C), and dominance—in diversity and abundance—by 11 families of angiosperms: Leguminosae, Moraceae, Annonaceae, Euphorbiaceae, Lauraceae, Sapotaceae, Myristicaceae, and Palmae represent ~50% of the diversity, whereas Leguminosae, Palmae, Rubiaceae, Violaceae, Euphorbiaceae, Meliaceae, Sapotaceae y Moraceae represent ~57% of all trees and shrubs. The forest is multistratified, with lianas and epiphytes and a closed canopy that is dominated by angiosperms. A high proportion of species have large leaves >4500 mm<sup>2</sup> (mesophylls), entire (smooth) margins, and drip-tips; the density of leaf venation has a bimodal distribution, with low density in the understory and high density in the canopy.

The development of Neotropical terrestrial communities can be divided into two major phases, Cretaceous and Cenozoic. During the Cretaceous, angiosperms originated and had a massive radiation (Crane & Lidgard, 1989; Magallón & Castillo, 2009; Magallón et al., 1999), terrestrial vertebrate communities were dominated by Dinosauria, CO<sub>2</sub> concentrations were high (>1000 ppm) (Royer, 2010; Royer et al., 2012), and by the middle Cretaceous, high mean annual temperatures were ~7 °C above modern values (Jaramillo & Cárdenas, 2013). In contrast, the Cenozoic is characterized by a complete dominance of angiosperms (Graham, 2010, 2011), massive radiations of mammals that expanded into a variety of habitats (Gingerich, 2006; Simpson, 1983), and the transition from a warm-mode climate to the pre-industrial cool-mode climate (Royer, 2016; Royer et al., 2012; Zachos et al., 2001).

## 2. Cretaceous

The oldest records of angiosperms in both high and low latitudes is Barremian (ca. 130 Ma); the fossil pollen *Clavatipollenites* has a worldwide distribution including Israel, England, equatorial Africa, and Argentina (Archangelsky & Taylor, 1993; Brenner, 1974; Doyle et al., 1977; Gübeli et al., 1984; Kemp, 1968) and *Walkeripollis*, a pollen that belongs to Winteraceae, is found in equatorial Africa (Doyle et al., 1990). The oldest records of megafossils (leaves, flowers, fruits) are *Archeofructus*

and *Leefructus* from the Aptian (ca. 122 Ma) of China (Sun & Dilcher, 2002; Sun et al., 2002, 2011). The first angiosperms were small, with reduced flowers and small seed size; they were opportunistic, early successional colonizers, probably living in aquatic habitats or near water bodies that were often submitted to disturbance (Doyle, 2012; Friis et al., 2015; Sun et al., 2002). A global meta-analysis of the Cretaceous paleobotanical record (Crane & Lidgard, 1989, 1990) showed that angiosperms gradually increased their diversity and abundance throughout the Cretaceous, and by the Maastrichtian, they surpassed other plant groups in diversity, including cycadophytes, pteridophytes (ferns), and Coniferales. This global analysis, however, lacked tropical megafossils and had very few sites with quantitative palynological data (Mejía-Velásquez, 2007). Thus, patterns of dominance, diversification, and distribution of forests within tropical zones during the Cretaceous still remain very unclear.

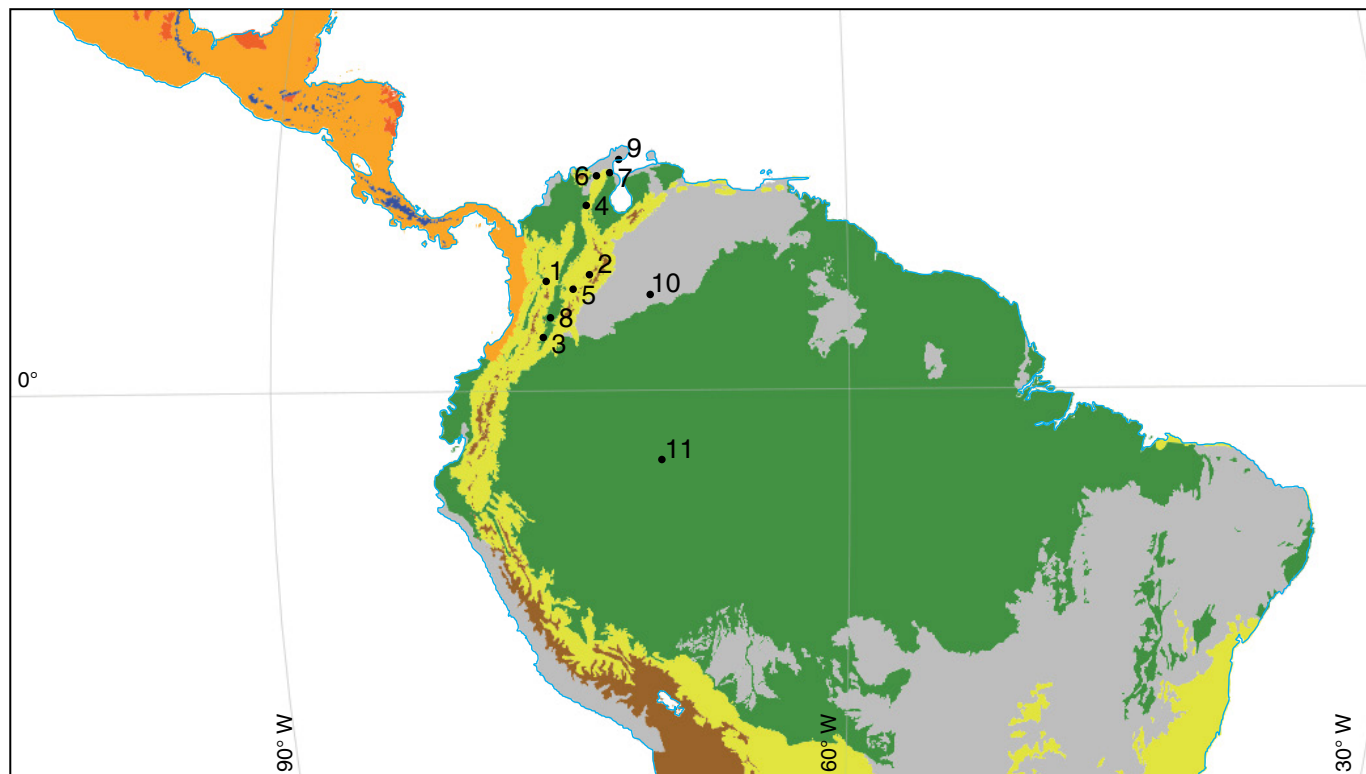
DNA-based phylogenies show a Jurassic (183 Ma) angiosperm origin (Bell et al., 2010; Wikström et al., 2001), and a rapid radiation of the major angiosperm orders during the Cenomanian (ca. 100–90 Ma) (Moore et al., 2010; Wang et al., 2009). Other genetic studies have shown that by the Cretaceous even many of the extant angiosperm families were already present (Bell et al., 2010; Davis et al., 2005). These phylogenies, however, are in stark contrast with the fossil record, which lacks angiosperms in pre-Cretaceous strata (Herendeen et al., 2017). It has been proposed that the molecular and fossil records can be reconciled if Jurassic angiosperms were restricted to the understory of rainforest habitats and did not radiate until the Cretaceous (Doyle, 2012). In contrast, some have suggested that heterogeneous rates of molecular evolution could push divergence ages in DNA-based analysis to appear much older than they truly are (Beaulieu et al., 2015). There is still a large disparity that needs to be solved, underscoring the importance of plant fossil data from tropical latitudes during the earliest Cretaceous and Jurassic.

The disparity between DNA and fossils also exists in the genesis of the rainforest structure. Molecular studies have suggested that Cenomanian tropical forests were already dominated by angiosperms (Wang et al., 2009) and were similar in structure to extant forests (Davis et al., 2005). However, the fossil record of the Cretaceous suggests otherwise. Multiple lines of evidence indicate that angiosperms did not dominate the biomass of most Cretaceous forests (Wing & Boucher, 1998). Angiosperm fossil wood is scarce compared to gymnosperm wood, indicating that most angiosperms did not occupy the canopy. Most angiosperm seeds were small (Wing & Boucher, 1998), indicating that the canopy was not closed, in contrast to modern multistratified forests where there is a large variance in seed size, a byproduct of the intense competition for light in a closed-canopy environment (Muller-Landau, 2010). Leaf venation density was much lower than in extant forests (Feild et al., 2011a), and even during the Maastrichtian

leaf density venation did not follow the pattern found in extant angiosperm-dominated forests (Crifò et al., 2014), suggesting the absence of a multistratified forest with a canopy dominated by angiosperms where the competition for light is intense. The fossil record of lianas, mainly Menispermaceae and Bignoniaceae, is very scarce, whereas it is abundant during the Cenozoic (Burnham, 2009; Doria et al., 2008; Jacques et al., 2011). In summary, angiosperms, although already diverse, did not dominate the forest biomass during the Cretaceous, neither in Neotropical nor in temperate regions.

One of the oldest Cretaceous records in tropical latitudes is the fossil flora of San Felix (Hauterivian, ca. 135 Ma), in Caldas, Colombia (González et al., 1977; Lemoigne, 1984) (Figure 1). Although it contains angiosperms, it has an abundance of Benettiales, ferns, Cycadales, and a few conifers (González et al., 1977; Lemoigne, 1984; Sucerquia & Jaramillo, 2008). Leaf morphology of the San Felix flora differs greatly from extant tropical leaves by having a much smaller leaf area and a lower leaf vein density (Feild et al., 2011a), indicating a lower photosynthetic capacity and therefore lower rates of biomass production. The Barremian – Aptian flora of Villa de Leyva (Figure 1), found in marine deposits, is composed mainly of ferns and cones of Cycadales and conifers (mainly Cupressoidae and Araucariaceae), which probably floated into the epicontinental Cretaceous seas. Many of these taxa are related to southern Gondwana clades (Huertas, 2003; van Waveren et al., 2002). Palynofloras from the Upper Magdalena Basin and the Llanos Foothills during the Albian – Aptian were dominated by pteridophytes and gymnosperms (mainly *Araucariacites*, cycads, and *Classopollis*), while angiosperm diversity was very low, an average of 3.7% per sample in the Aptian and 3.3% in the Albian. Abundance was also low (7.2% for the Aptian, 5.3% for the Albian) (Mejía-Velásquez, 2007; Mejía-Velásquez et al., 2012) (Figure 1). The abundance of humidity indicators was higher than that of aridity indicators (61% versus 10%) (Mejía-Velásquez et al., 2012), suggesting that northwestern Gondwana had humid climates during the Aptian – Albian contrary to the widespread aridity that had been assumed for the tropical belt (Herngreen et al., 1996). Furthermore, there was an inverted latitudinal diversity gradient during the Albian—the tropics had fewer species than the temperate regions even though the rate of floristic turnover was higher (Mejía-Velásquez et al., 2012). Perhaps the modern steep latitudinal diversity gradient is an intrinsic angiosperm property.

During the Cenomanian, the low dominance of angiosperms continued and a group of gymnosperms, Gnetales, significantly increased its diversity and abundance (Herngreen & Dueñas, 1990; Herngreen et al., 1996), although the high abundance and diversity of ferns still continued, suggesting that humid conditions in northwestern Gondwana prevailed, in agreement with some hydrological models (Ufnar et al., 2002, 2004, 2008). Angiosperm pollen morphology became more variable, sim-



**Figure 1.** Extant terrestrial biomes of Colombia following the classification given in Figure 2. Biomes distribution was derived from the WWF global ecoregion map (Olson et al., 2001). Sites described in the manuscript include: **(1)** San Felix, **(2)** Villa de Leyva, **(3)** Upper Magdalena Valley (Mejía-Velásquez et al., 2012), **(4)** Cretaceous/Paleocene (De la Parra, 2009), **(5)** Guaduas (Martínez et al., 2015), **(6)** Cerrejón, **(7)** PETM (Jaramillo et al., 2010b), **(8)** Villavieja, **(9)** Ware, **(10)** Llanos, and **(11)** 105-AM (Jaramillo et al., 2017b).

ilar to the pattern seen in North America (Doyle & Hickey, 1976; Lupia et al., 1999), although it still needs to be properly quantified. No Cenomanian tropical macrofloras have been discovered, and they are highly needed as this is a critical time for angiosperm evolution.

Peak temperatures of the last 140 Ma occurred during the Cenomanian – Turonian transition (Bice et al., 2006), when the tropics were 7 °C warmer than modern values (Jaramillo & Cárdenas, 2013) and CO<sub>2</sub> levels were >1000 ppm (Royer, 2006). Eustatic sea level also reached the maximum levels of the past 140 Ma, producing epicontinental seas as extensive continental areas were flooded (Haq et al., 1988; Miller et al., 2005). By the early Turonian, the abundance and diversity of Gnetales in the Neotropics had greatly diminished, but it is still uncertain whether this reduction was gradual or abrupt.

The Late Cretaceous (90–66 Ma) is characterized by a gradual reduction of global temperatures together with a reduction of CO<sub>2</sub> levels, but information about tropical forests during most of this period is scarce. During the Maastrichtian (70–66 Ma), sea level started to drop rapidly and extensive coastal plains covered with forests developed (Nichols & Johnson, 2008). The Maastrichtian paleoflora of the Guaduas (Figure 1) and Umir Formations indicates a co-dominance of angiosperms, cycads, gymnosperms (Araucariaceae), and

pteridophytes (ferns). The palynological record indicates that the angiosperms and ferns co-dominated, with angiosperms representing ~50% of assemblages (De la Parra et al., 2008a, 2008b), a pattern that is also seen in the Oleanane/Opene biomarker record (Rangel et al., 2002). Although several angiosperm families had been present here, including Palmae, Annonaceae, Lauraceae, Piperaceae, Rhamnaceae, many others had uncertain affinities (Correa et al., 2010; García, 1958; Gutiérrez & Jaramillo, 2007; Martínez et al., 2015; Sarmiento, 1992; Sole de Porta, 1971). Most Maastrichtian fossil seeds are small, and Menispermaceae and Bignoniaceae, families with high abundance of lianas, are missing. Overall, Guaduas still does not correspond to a Neotropical forest floristically. Guaduas leaf venation density also does not show the bimodal distribution of extant forests, suggesting that the canopy was not fully closed yet (Crifò et al., 2014), although it had already large leaves with entire margins and drip-tips similar to extant forests (Feild et al., 2011a). Neotropical Maastrichtian forests follow the same pattern as coetaneous forests from Nebraska, where angiosperms were the dominant element in floodplains, similar to the environment of the Guaduas deposits, but gymnosperms and ferns dominated in all other habitats (Wing et al., 1993). Angiosperms were mostly herbaceous and had only a 12% of the dominance overall (Wing et al., 1993).

Both forest composition and structure changed radically following the impact of a meteorite in the Yucatán peninsula and the associated climatic events (Nichols & Johnson, 2008; Schulte et al., 2010). The Colombian palynological record indicates a 75% plant extinction of late Maastrichtian taxa (De la Parra, 2009) (Figure 1), an extinction level higher than in North America, where the palynological extinction levels reached ~30% (Hotton, 2002). By the Paleocene, as we will see next, the flora already resembled that of extant forests.

This floristic change could have had climatic consequences as well. Nowadays, a large component of the precipitation over Amazonia is produced by forest evapotranspiration (Wright et al., 2017), driven by the high photosynthetic capacity of angiosperms, much higher than gymnosperms (Boyce & Lee, 2010). Angiosperm venation density in the Cretaceous is generally low, and not much higher than gymnosperms (Feild et al., 2011a, 2011b), but at the onset of the Cenozoic, leaf vein density increases considerably to levels similar to extant forest (Crifò et al., 2014; Feild et al., 2011a). Experiments of climate sensitivity have shown that replacing an angiosperm forest with a conifer forest in Amazonia generates higher mean annual temperatures (3 °C), a 30% drop in annual precipitation, and an increase in the length of the dry season by two months, changes that are mostly due to the lower venation density of gymnosperms and associated lower photosynthetic and evapotranspiration rates (Boyce & Lee, 2010). This suggests that the change in landscape occupancy at the Cretaceous – Cenozoic transition, from a forest dominated by conifers and ferns to one of angiosperm dominance, transformed the tropical climate to being more humid, less warm, and less seasonal.

Why was angiosperm success and radiation in the Cretaceous so closely associated with disturbed and flooded environments? That is still an unsolved question. One hypothesis suggests that the time needed to generate the pollen tube, a critical step in seed production, is part of the answer. While the pollen tube in gymnosperms takes a long time to be generated, over a year in some cases, angiosperms produce it much faster, even in less than two hours (Williams, 2008). Angiosperms therefore might have been able to produce more seeds at a faster rate than gymnosperms, and this could have been an advantage in flooded and disturbed ecosystems, where the landscape is often changing and plants must grow fast and produce seeds quickly before the next flooding event occurs.

Overall, the fossil record suggests that Neotropical Cretaceous forests lacked multistratification and canopy was open and dominated by gymnosperms. Most angiosperms were shrubs or small plants, ruderals, dominating both floodplains and forest gaps but not most of the landscape. A historical accident, a meteorite collision, permanently changed the structure and composition of the tropical forests, thus delaying the ecological success of the angiosperms following their origination during the Early Cretaceous by 55 my.

### 3. Paleogene

Neotropical floras of the Paleocene were already dominated by angiosperms (~80% of palynoflora) (De la Parra, 2009; Doubinger, 1973; Jaramillo et al., 2006, 2007; Pardo–Trujillo, 2004; Pardo–Trujillo & Jaramillo, 2002; Pardo–Trujillo et al., 2003; van der Hammen, 1958), as is also indicated by biomarkers (Rangel et al., 2002), a foliar physiognomy typical of tropical forests (entire margins, large leaves, and drip-tips) (Wing et al., 2009), and a floristic composition similar to modern Neotropical forests including Fabaceae, Moraceae, Annonaceae, Euphorbiaceae, Lauraceae, Sapotaceae, Arecaceae, Araceae, Flacourtiaceae, Anacardaceae, Tiliaceae, and Meliaceae (Carvalho et al., 2011; Doria et al., 2008; Gómez–Navarro et al., 2009; Herrera et al., 2008; Jaramillo et al., 2007, 2014a; Pons, 1988; Wing et al., 2009). Forests also have abundant Menispermaceae (Doria et al., 2008), a family rich with lianas; this, together with the bimodal distribution of leaf venation density (Crifò et al., 2014; Feild et al., 2011a) and a high variance in seed size reaching up to 20 cm (Gómez–Navarro et al., 2009; Herrera et al., 2011, 2014b; Stull et al., 2012), indicates that the Paleocene forests were competing for light and the canopy was closed and dominated by angiosperms, characteristics of a multistratified forest. The high abundance of Fabaceae in the Paleocene, the most abundant family of trees/shrubs in all extant tropical forests (Ricklefs & Renner, 2012) but absent from the Cretaceous record, also indicates a profound transformation of the forest across the Cretaceous – Paleocene boundary. There are also aquatic ferns including *Salvinia* (Pérez–Consuegra et al., 2017). This large body of information about Paleocene forests comes mainly from the fossil record of the Cerrejón Formation gathered at the Cerrejón Coal mine (Figure 1), the largest open-pit coal mine in the world, which offers large-scale exposures (Jaramillo et al., 2014a). The fauna indicates a productive ecosystem: freshwater turtles up to 2 m long and related to the charapas of the Orinoco Basin; several species of crocodiles, mostly Dyrosauridae, some reaching 12–15 m; snakes related to boas reaching 13–15 m in length and 1 m in diameter; 2-m-long lungfishes; and several mollusks (Bayona et al., 2011; Cadena & Jaramillo, 2006; Cadena & Schweitzer, 2014; Cadena et al., 2012a, 2012c; Hastings et al., 2010, 2011, 2014; Head et al., 2009a, 2009b). In 16 years of exploration, no mammals have been found, suggesting that they were scarce. The Cerrejón deposits represent the oldest multistratified tropical forest known, similar to extant rainforests but with two marked differences. First, the mean annual temperature was ~1.5–2 °C higher than in extant forests and CO<sub>2</sub> was almost double (~500 ppm) (Royer, 2010). Mean annual temperature in Cerrejón and nearby areas has been estimated at ~29 °C using a variety of techniques including TEX<sub>86</sub> (Jaramillo et al., 2010b), leaf margin analysis (Peppe et al., 2011; Wing et al., 2009), and snake paleothermometry (Head et al., 2009a, 2009b). The

second difference is a significantly lower plant diversity than in extant forests (Jaramillo et al., 2007; Wing et al., 2009), which is accompanied by a lower abundance of specialized herbivores (Carvalho et al., 2014; Wing et al., 2009). This difference could be explained by soil control, as the water table in Cerrejón probably was very high all year long. However, this low Paleocene diversity is observed in the palynological record throughout Colombia and Venezuela across a wide variety of depositional settings (Jaramillo, 2002; Jaramillo & Dilcher, 2000, 2001; Jaramillo et al., 2006, 2010b). An alternative hypothesis is that recovery following the K–Pg mass extinction was slow and took several million years to reach prior diversity levels, as has been observed in others mass extinctions (Erwin, 2008).

At the onset of the Eocene, a short-lived (ca. 200 ky) warming event known as the PETM (Paleocene Eocene Thermal Maximum) occurred (McInerney & Wing, 2011). Beginning ca. 56.3 Ma, temperature increased globally 5–7 °C over ca. 10 000–50 000 years (Frieling et al., 2017; Kennett & Stott, 1991; Westerhold et al., 2009; Zachos et al., 2003). The rapid and intense warming was produced by the addition to the atmosphere of ~10 000 Pg of carbon during a 50 ky interval, derived from volcanism in the North Sea (Gutjar et al., 2017); this input is roughly equivalent to adding 1300 ppm of CO<sub>2</sub> to a Paleocene atmosphere that had ~500 ppm of CO<sub>2</sub>. The PETM is the most rapid addition of CO<sub>2</sub> to the atmosphere over the past 140 million years and produced a greenhouse effect similar to the warming we are currently experiencing but at a rate ten times slower than today (McInerney & Wing, 2011). It is estimated that by the year 2250, we will reach ~2000 ppm of CO<sub>2</sub>. In other words, in just 400 years we will have increased CO<sub>2</sub> to the same levels that it took 50 000 years to reach following the onset of the PETM.

The PETM is a good analogue for understanding the consequences of our ongoing warming. The main process that can effectively remove CO<sub>2</sub> from the atmosphere is weathering of carbonates and silicates, but this is a process that operates at geological scales. During the PETM, it took ca. 180 000 years to return to previous levels (Bowen & Zachos, 2010). For our modern climate, and assuming that no more CO<sub>2</sub> is added, it would take geological time—thousands of years—to return to preindustrial values (Archer et al., 2009). After 1000 years, 25 to 60% of the injected CO<sub>2</sub> would still remain in the atmosphere (Archer et al., 2009). Was discovered in the deep ocean by the Ocean Drilling Project (Kennett & Stott, 1991; Westerhold et al., 2009; Zachos et al., 2003). At the Paleocene–Eocene boundary, marine paleontologists had long recognized a stratigraphic interval where all carbonate was dissolved; this interval was also associated with a negative excursion of ~4–5 ‰ in δ<sup>13</sup>C. The same interval was later recognized in terrestrial sediments worldwide (Wing et al., 2005). Both changes in this interval could only be explained by a massive release of carbon with negative values of δ<sup>13</sup>C. Several hypotheses have been

proposed to explain the source of this carbon and the subject is still controversial (McInerney & Wing, 2011). One proposed source is the release of methane hydrates that are trapped at the bottom of the ocean and contain massive amounts of carbon. About ~2500 to 4500 Gt of highly <sup>13</sup>C–depleted marine methane clathrates that rapidly oxidizes to CO<sub>2</sub> (Bralower et al., 1997; Dickens et al., 1995, 1998), increasing CO<sub>2</sub> by ~500 ppm (Gehler et al., 2016). However, the volume of methane trapped in the hydrates is still uncertain. Another explanation, which has recently received large support, is the massive release of CO<sub>2</sub> by North Sea volcanism (Gutjar et al., 2017).

Whatever the source, the PETM produced large changes in the ocean with a massive extinction of benthic foraminifera (Thomas & Shackleton, 1996) and radiations of planktonic foraminifera. On land, changes were even more drastic. Most modern mammal orders originated during the PETM, including artiodactyls (deer), perissodactyls (horses), and primates (excluding plesiadiforms), and these quickly dispersed across Asia, Europe, and North America (Clyde & Gingerich, 1998; Gingerich, 2006). The effect on plants was diverse; for example, in midlatitudes such as Wyoming (midwestern USA), there is rapid immigration by southern angiosperms, which replaced the existing vegetation of conifers and angiosperms (Wing et al., 2005). This PETM vegetation also experienced more intense herbivory than the pre–PETM floras (Currano et al., 2008). Once the event ended, the pre–PETM flora returned to Wyoming and replaced the immigrant vegetation.

In this process, there are very few originations or extinctions and most of the changes are the product of migrations. In the Neotropics the effects of the PETM were different (Figure 1). The fossil record of three sites in northeast Colombia and northwest Venezuela indicated that the mean annual temperature increased ~3.5 °C during the PETM (Jaramillo & Cárdenas, 2013; Jaramillo et al., 2010b), similar to the increase in oceanic temperatures of tropical oceans (Frieling et al., 2017; Zachos et al., 2003). The vegetation rapidly became more diverse, by about 30%, with the addition of a new group of taxa (Jaramillo et al., 2010b), e.g., *Tetracolporopollenites maculosus* (Sapotacea), *Retitrescolpites? irregularis* (Phyllantacea), *Striatopollis catatumbus* (Fabaceae), *Margocolporites vanwijhei* (Fabaceae). Extinction rates did not change while origination rates doubled, with many taxa appearing for the first time all across the Neotropics, suggesting that these new taxa were a product of evolution rather than migration from other latitudes. This radiation can also be seen in DNA–based phylogenies of many tropical clades, including epiphytic ferns, typical of Neotropical forests, orchids, and leaf–cutter ants (Ramírez et al., 2007; Schuettelpelz & Pryer, 2009; Schultz & Brady, 2008). There is also no evidence of an increase in aridity, but plant water use became more efficient due to high concentrations of CO<sub>2</sub>, as seen in the deuterium isotopic record (Jaramillo et al., 2010b); similar results

have been seen in greenhouse experiments with extant plants (Cernusak et al., 2011, 2013).

These results contradict paleoclimatic global models that predict temperatures  $>45^{\circ}\text{C}$  for most of the Neotropics and a major collapse of Neotropical vegetation due to heat stress (Bowen & Zachos, 2010; Huber, 2008; Huber & Caballero, 2011; Huber & Sloan, 2000). In order to simulate the PETM, climatic models add large volumes of  $\text{CO}_2$  to the atmosphere (Huber & Sloan, 1999; Huber et al., 2003; Shellito et al., 2003; Sloan & Barron, 1992; Sloan & Morrill, 1998; Sloan & Rea, 1996; Sloan & Thomas, 1998; Sloan et al., 1995), making the tropical temperature too hot compared to empirical data. There must be a mechanism, still unknown, that is heating poles at a much higher pace than the tropics during periods of global warming.

The rapid ending of the PETM is also an enigma. The PETM ends ten times faster than expected by the standard rates of the weathering process (Bowen & Zachos, 2010). One hypothesis is that both onset and termination of the PETM were facilitated by the collapse of the tropical vegetation (Bowen & Zachos, 2010; Huber, 2008). However, the empirical record demonstrates that tropical vegetation did not collapse during the PETM and that plant water use efficiency (WUE) increased (Jaramillo et al., 2010b). The WUE is the proportion of water that the plant uses for photosynthesis and to produce biomass versus the proportion of water that is lost by transpiration. An increase in WUE at the continental scale could indirectly promote capture of atmospheric  $\text{CO}_2$  in two ways: first, it could have increased biomass production (this effect is seen in diversity, as there is strong correlation between biomass and diversity). Second, it could decrease the water that the plant transpires, this “excess” water not used by the plant could therefore reach the water-table and the drainage systems, raising the weathering potential and thus increasing the trapping of atmospheric  $\text{CO}_2$  (De Boer et al., 2011; Lammertsma et al., 2011). In summary, tropical forests could have facilitated the termination of the PETM by increasing biomass production and accelerating weathering, both of which quickly trapped atmospheric  $\text{CO}_2$ .

From the Eocene (56 Ma) to the early Miocene (ca. 16 Ma), global temperature varied greatly, with a gradual increase during the early Eocene until it peaked during the Early Eocene Thermal Maximum (ETM), which began at the end of the early Eocene and lasted until the start of the middle Eocene. Following the ETM, there is a long and slow drop in temperature during the middle and late Eocene. At the Eocene – Oligocene transition, ca. 34 my ago, there is sharp cooling that is coetaneous with the earliest glacial development in Antarctica (Anderson et al., 2011; Liu et al., 2009; Zachos et al., 2001). First glaciations in Antarctica appear to be correlated with the onset of South America’s separation from Antarctica, which made possible a circumpolar current and thus the cooling of Antarctica. However, some models have not been able to reproduce a massive glacial buildup in Antarctica without a sharp

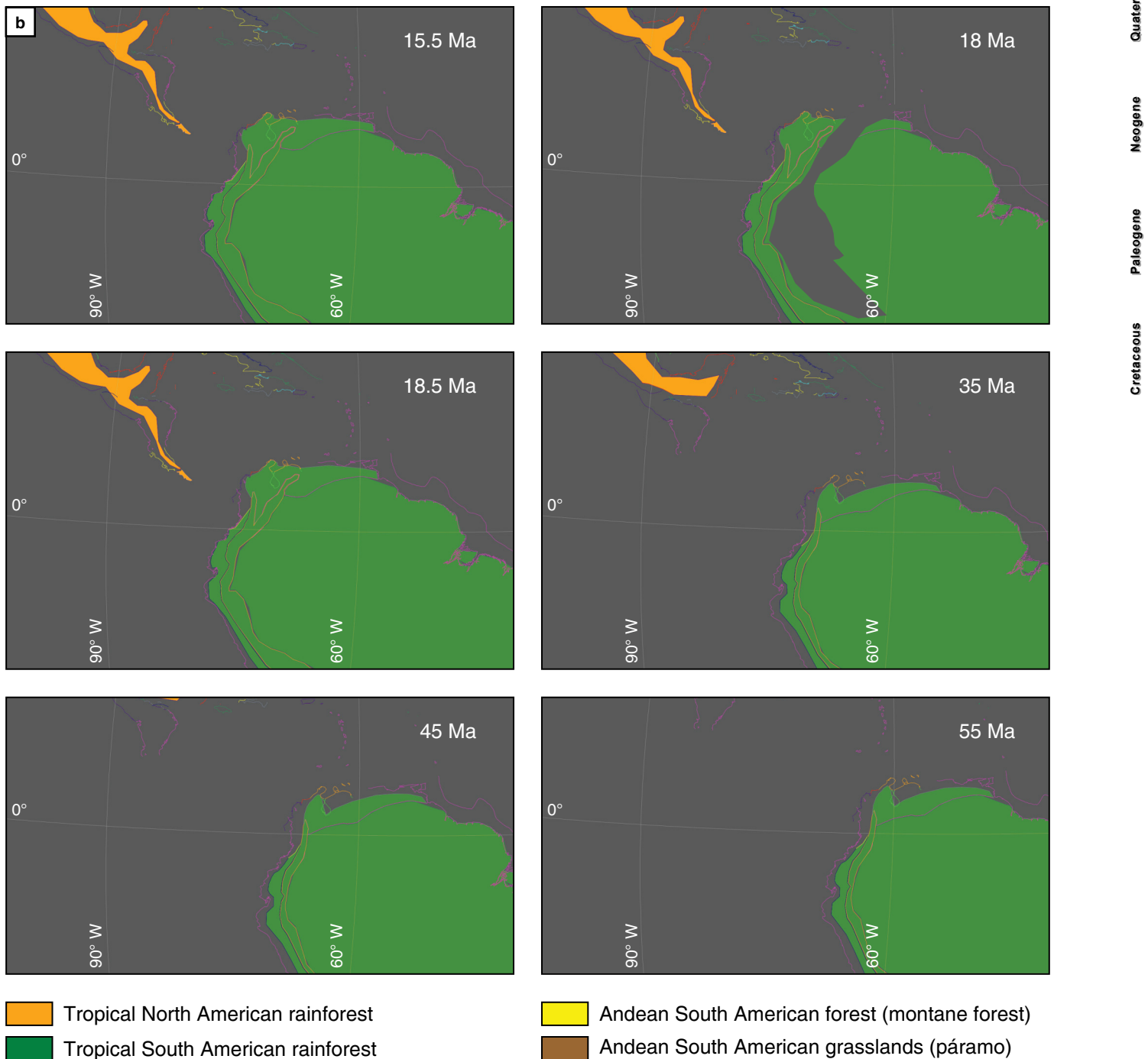
drop in  $\text{CO}_2$  below a threshold value of  $\sim 450$  ppm (Lefebvre et al., 2012), values that are not reached until the Pliocene. It seems then, that the extensive modern Antarctic glacial cover is a recent phenomenon, probably occurring within the last 5 my (Anderson et al., 2011). As further evidence, the evolution of antifreeze glycoproteins in Antarctic notothenioid fishes, which are uniquely adapted to freezing waters, occurs only during the late Neogene (Near et al., 2012), and the distribution of the limpet *Nacella* was also recently established (González-Wevar et al., 2016).

During the Oligocene, global temperatures remained largely stable, with a small warming at the end of the Oligocene that was followed by another cooling at the onset of the Miocene (Zachos et al., 2001). The overall trend in the diversity of the Neotropical forest follows the same variations as the global temperature, increasing during warming periods and dropping during cooling intervals (Jaramillo & Cárdenas, 2013; Jaramillo et al., 2006). This relation could reflect the positive effect of temperature increases on rates of molecular mutations (Wright et al., 2006) and on biotic interactions, including herbivory, due to higher energy in the system (Jaramillo & Cárdenas, 2013). Some authors have proposed that Neotropical forests expanded during global warmings, thus increasing diversity by the area–diversity effect (larger area leads to more species) (Fine & Ree, 2006; Fine et al., 2008; Rosenzweig, 1995). However, the empirical paleobotanical record of South America shows that Neotropical forests do not expand beyond the tropical latitudes during warmings, especially the early Eocene warming (Jaramillo & Cárdenas, 2013) (Figure 2b). Instead, a non-analogue biome, the “mixed forest,” occupied most of the temperate regions during warming events. This biome does not exist nowadays, as temperate regions are much cooler today than in the early Eocene (Hinojosa & Villagrán, 2005).

Several authors have predicted that tropical terrestrial ecosystems will collapse as a consequence of the ongoing climate warming, under the assumption that the extant tropical vegetation lives close to its climatic optimum (Huber, 2008; Stoskopf, 1981; Tewksbury et al., 2008). Several deleterious effects in plants are observed when temperature rises, including an increase in respiration that decreases net production, a decrease in photosynthesis, and increases in photoinjuries, leaf stress, and the emission of isoprenes (Bassow et al., 1994; Cernusak et al., 2013; Huber, 2008, 2009; Lerdaud & Throop, 1999; Lewis et al., 2004; Stoskopf, 1981; Tewksbury et al., 2008), although recent studies have shown that the upper thermal stress of canopy leaves is  $\sim 50\text{--}53^{\circ}\text{C}$  (Krause et al., 2010) and tropical trees can acclimate very fast (Slot & Winter, 2017). How to explain that tropical plants did not collapse during past global warmings but rather increased in diversity and biomass? Leaf temperature, a critical factor for plants, mainly depends on three factors: air temperature, levels of atmospheric  $\text{CO}_2$ , and soil moisture. The combination of all three factors deter-







**Figure 2.** Terrestrial biome reconstruction for the past 55 my of the Neotropics. **(a)** Reconstruction from 0 to 14 Ma. **(b)** Reconstruction from 15.5 to 55 Ma. The reconstruction is an orthographic projection based on the plate tectonic model of GPlates 1.5.0, using the plate reconstruction of Seton (Seton et al., 2012). Terrestrial biomes include the tropical rainforest, which was divided into South America and North American (Central American) rainforests; the montane forest (forest > 2000 m of elevation), which is divided into the Andean South American forest and the Central American Montane forest; the Andean South American grasslands (or páramos, grasslands above the tree line in the Andes of South America); and the tropical South and North American savannas, which includes the xerophytic forests. Terrestrial biomes adapted from Jaramillo & Cárdenas (2013) and Jaramillo (2018). The exhumation evolution of the Isthmus of Panamá from the Montes models (Farris et al., 2011; Montes et al., 2012a, 2012b, 2015) (*continued*).

mines a plant's response to ambient temperature. Warming events during the Cretaceous and Paleogene are characterized by elevated levels of CO<sub>2</sub> together with high precipitation (Ja-

ramillo et al., 2010b; Royer, 2010; Ufnar et al., 2002, 2004, 2008; Wing et al., 2009) and short dry seasons (Jaramillo et al., 2010b). Physiological studies indicate that plants are more

efficient at photosynthesis at higher temperatures (up to 10 °C) provided that levels of both CO<sub>2</sub> and soil moisture are high (Aber et al., 2001; Berry & Björkman, 1980; Lloyd & Farquhar, 2008; Niu et al., 2008). Furthermore, WUE increases when levels of CO<sub>2</sub> increase (Cernusak et al., 2011). The genes that regulate photosynthesis are deeply rooted in plant phylogeny and it would be expected that photosynthesis in Eocene and Paleocene plants was fundamentally the same as in extant plants. The plant fossil record of the Neotropics suggests, therefore, that modern plants might already have the genetic variability to cope with increases in temperature and CO<sub>2</sub>, as some have proposed (Lloyd & Farquhar, 2008).

#### 4. Neogene

The Neogene represents a new chapter in the history of tropical biomes with the dramatic expansion of several biomes including savannas, dry forests, xerophytic forests, deserts, montane forests, and páramos (Figure 2a, 2b). Today, savannas occupy 30% of land on earth. They provide most of the food we consume and most of the land we inhabit (Jacobs et al., 1999). Grasses of tropical savannas comprise <2% of plant species (Sage et al., 1999), but nevertheless capture 20% of terrestrial carbon (Lloyd & Farquhar, 1994). Despite the importance of savannas, we still know very little about their origin and the factors that control them, especially in the South American tropics (Edwards et al., 2010).

The main factor that determines the type of vegetation within tropical lowland is precipitation rather than temperature. Variations in mean annual temperature within the tropical zone are minimal, from 23 to 28 °C, with very low variations throughout the year. In contrast, there are drastic variations in precipitation, both in the total amount throughout the year and in the length of the dry season. Biomes change as precipitation conditions changes (Jaramillo & Cárdenas, 2013; Lehmann et al., 2011), shifting from humid forest to dry forest, savanna, xerophytic forest, and desert as precipitation decreases (Jaramillo & Cárdenas, 2013). Another important factor during the Neogene is diminishing CO<sub>2</sub> levels. This trend began at the start of the Oligocene (ca. 34 Ma) and continued until the onset of the Pleistocene when CO<sub>2</sub> levels reached <200 ppm during glacial times (De Boer et al., 2010; Royer, 2006, 2010; Royer et al., 2011). There is a rapid increase during the middle Miocene climatic optimum (MMCO) ca. 17–14 Ma, characterized period of relative warmth, with global mean surface temperatures likely increasing by 2–3 °C (Zachos et al., 2001), and another during the late Pliocene (5–3 Ma) also characterized by warmer temperatures (Filippelli & Flores, 2009; Ravelo et al., 2006). During the glacial/interglacial times of the last 2.6 my, CO<sub>2</sub> has oscillated in concordance with global temperature, ranging from ~280 ppm during interglacial periods to 180

ppm during glacial periods (Lüthi et al., 2008; Monnin et al., 2001; Siegenthaler et al., 2005; Tripathi et al., 2009).

Four main groups of plants are characteristic of dry environments: Cactaceae, Agavaceae, Poaceae, and the so-called “ice plants” of South Africa (Arakaki et al., 2011). Many of them have one of two paths for photosynthesis, either C4 or CAM, whereas most trees use C3 photosynthesis. Photosynthetic pathways C4 and CAM are much more efficient than C3 in areas where temperature is very high and there is hydric stress and/or low CO<sub>2</sub> levels (Edwards et al., 2010). Under such conditions, C3 photosynthesis becomes difficult because the water-loss by transpiration is too high (Edwards et al., 2010). The phylogeny of the aforementioned groups of plants indicates that they originated towards the end of the Eocene/beginning of the Oligocene, probably associated with the pronounced global decrease in CO<sub>2</sub> at the end of the Eocene, ca. 34–36 Ma (Arakaki et al., 2011). However, their radiation occurred millions of years later, during the late Miocene to Pleistocene (Arakaki et al., 2011; Edwards et al., 2010). This phylogenetic radiation seems to coincide with the expansion of the area occupied by savannas, as deduced from the fossil record.

Savanna expansion appears not to be coeval on a global scale, although the fossil record is still scarce (Edwards et al., 2010). Most empirical data indicate that 15 my ago savannas had not yet expanded (Edwards et al., 2010) (Figure 2a). In Kenya, the expansion of the savannas with C4-Poaceae occurs around 6–8 Ma (Uno et al., 2011). In Pakistan, the savannas C4 expand around 7 Ma (Morgan et al., 1994). In the Neotropics, the information about when the savannas developed is scarce (Wijmstra & van der Hammen, 1966). Areas that nowadays correspond to xerophytic/dry forests and savannas, like the Upper Magdalena Valley (Villavieja) (Figure 1), were humid forests 13–11 my ago (Kay et al., 1997) (Figure 2a). In Falcón province, northwestern Venezuela, fossil records of the upper Miocene (ca. 9 Ma) indicate the presence of a more humid forest, very different from the xerophytic vegetation present in the region today (Aguilera, 2004; Díaz de Gamero & Linares, 1989; Hambalek, 1993; Hambalek et al., 1994; Linares, 2004; Quiroz & Jaramillo, 2010; Sánchez-Villagra & Aguilera, 2006). The fossil record of the late Neogene and Quaternary in the Llanos Orientales of Colombia has mostly focused on the Holocene (Wijmstra & van der Hammen, 1966). Palynofloras of the Miocene, up to ca. 6 Ma, indicate that the region was not a savanna (Jaramillo et al., 2006, 2017b), therefore, the expansion of the savannas in the north of South America must have occurred very recently, at some point over the past 6 my (Figures 1, 2a).

What factors could have induced the expansion of the savanna in the Neotropics? The amount of precipitation, as well as its seasonality, determines in large part the presence of savannas (Lehmann et al., 2011). Precipitation on a macroscale in northern South America is controlled by the amplitude and

migration of the intertropical convergence zone (ITCZ). When summer occurs in the Southern Hemisphere, the ITCZ migrates to the south and positions itself over southern Colombia, Ecuador, and the basin of the Amazon (Poveda et al., 2006), leaving large portions of northern South America under dry conditions. Precipitation increases over northern South America when the ITCZ migrates north during the boreal summer (Poveda et al., 2006). This shift of the ITCZ produces a long dry season over the region occupied by savannas and xerophytic forests in northern South America. Therefore, the ITCZ must have shifted at some point within the last 6 my in order to yield the modern climate configuration.

Two mechanisms affecting the ITCZ have been proposed. First, the closure of the isthmus of Panamá during the late Pliocene, 4.2–3.5 Ma, enhanced the thermohaline circulation, which pushed the ITCZ southward to its modern position (Billups et al., 1999; Chaisson, 1995; Chaisson & Ravelo, 1997; Haug & Tiedemann, 1998; Haug et al., 2001; Hovan, 1995; Keigwin, 1982; Mikolajewicz et al., 1993). However, recent studies indicate that the onset of the thermohaline circulation was ca. 10–12 Ma, a consequence of the closure of the Central American Seaway (Bacon et al., 2015a; Jaramillo, 2018; Jaramillo et al., 2017a; Montes et al., 2015; Sepulchre et al., 2014). Second, the onset of permanent extensive ice in the Northern Hemisphere at 2.6 Ma would have pushed the ITCZ south to its current position (Chiang & Bitz, 2005; Flohn, 1981; Shackleton et al., 1984).

An additional element that may have influenced the expansion of the savannas is the uplift of the Andes (Figure 2a). Models of climate sensibility (Sepulchre et al., 2010) indicate that the uplift of the northern Andes above 2000 m augmented the seasonality of northern South America, which could have facilitated expansion of the Neotropical savannas. Something similar occurred in southern South America, where precipitation from the Pacific Ocean is blocked by the western side of the Andes, enhancing the aridity in Patagonia (Sepulchre et al., 2010). Models of climate sensitivity have also shown that the rising the Central Andes above 2500 m may have intensified the Humboldt Current (Sepulchre et al., 2009). This current plays an important role in the regulation of the depth of the thermocline and the temperature of surficial waters of the eastern Pacific. Changes in the intensity of the Humboldt Current and/or in the depth of the thermocline in the tropical Pacific generate variations in the distribution and intensity of the atmospheric convection cells (circulation of Walker and Hadley), affecting the latitudinal position and intensity of the ITCZ over the eastern Pacific (Chiang, 2009; Martínez, 2009; Rincón-Martínez et al., 2010).

The uplift of the Andes also produced substantial modifications in the landscape. While the majority of the riverine flux was northbound during most of the Cenozoic, the uplift of the Andes shifted the hydrographic system towards the east, producing the modern configuration of the Amazon and Orinoco

hydrographic basins (Figueiredo et al., 2009; Hoorn, 1994a, 1994b; Hoorn et al., 1995, 2010, 2017; Jaramillo et al., 2010a). The process of uplifting also caused significant modifications in the patterns of subsidence across all Amazonian basins. The dynamic topography generated by the uplift/subsidence produced extensive floodplains in western Amazonia during most of the Cenozoic that, during the late Miocene, were shifted to the modern system of incisive rivers and reduced floodplains (Latrubesse et al., 2010; Sacek, 2014; Shephard et al., 2010).

Nowadays, floodplains constitute only 20% of the Amazon region (Toivonen et al., 2007), but during the Miocene they were much more extensive, allowing the existence of large reptiles and mammals, such as 3-m-long turtles (*Stupendemys*), crocodiles over 14 m long (*Purussaurus*), and rodents (*Phoberomys*) more than 1.8 m in length and weighing 700 kg (Antoine et al., 2007; Cozzuol, 2006; Frailey, 1986; Kay et al., 1997; Sánchez-Villagra, 2006; Sánchez-Villagra & Aguilera, 2006; Sánchez-Villagra et al., 2003). This high-subsidence system is called Pebas, and it is a biome that does not have a modern analogue (Jaramillo et al., 2017b), but it is closely related to the rainforest (Figure 2a). It is dominated by a unique depositional environment, termed “marginal,” that includes greenish to gray-colored, laminated, bioturbated, and locally fossil-rich mudstones coarsening up to very fine to medium-grained sandstones with coal interbeds. The association of these lithofacies represents accumulation on deltaic plains, low-energy wetlands with swamps, ponds, and channels, and shallow fresh-water lacustrine systems (Jaramillo et al., 2017b) (Figure 1). Associated with the high-subsidence system, and probably eustasy, are two distinct marine intervals in the Llanos Basin, an early Miocene interval that lasted ca. 0.9 my (18.1 to 17.2 Ma) and a middle Miocene interval that lasted ca. 3.7 my (16.1 to 12.4 Ma) (Figure 2a). These two marine intervals are progressively later toward the southern basins of western Amazonia, and in the Amazonas/Solimões Basin are much shorter in duration, ca. 0.2 my (18.0 to 17.8 Ma) and ca. 0.4 my (14.1 to 13.7 Ma), respectively (Jaramillo et al., 2017b). The Miocene lake systems that are produced all along the Magdalena valley, e.g., La Cira beds and the Barzalosa Formation, may also be related to these two marine flooding periods but correlations are still uncertain. The disappearance of the Pebas system occurred at ca. 10–11 Ma (Jaramillo et al., 2017b), concomitant with the onset of the Amazon River (Hoorn et al., 2017). This major shift probably precipitated the extinction of flora associated with the “marginal” environment of the Pebas systems and its fauna of large reptiles and abundant mollusks.

The Andes reached their modern elevation by the end of the Miocene (ca. 5–6 Ma; Garzzone et al., 2006, 2008, 2014; Ghosh et al., 2006; Kar et al., 2016; Wallis et al., 2016), thus generating two brand new biomes, the páramo and the cloud (montane) forest (Figure 2a). The species composition of these two biomes is roughly 50% derived from lowland tropical plants (tropical

Gondwanan lineages), ~25% from temperate latitudes in South America (temperate Gondwanan lineages), and ~25% from temperate latitudes in North America (temperate Laurasian lineages) (Gentry, 1982a, 1982b). The slopes of the Andes have also been considered a sort of engine of speciation because the topographic complexity generates diverse microenvironments (Gentry, 1982a; Hoorn et al., 2010). The history of the vegetation of the Andes during the late Neogene has been studied by professor van der Hammen and his team for more than four decades (Hooghiemstra & van der Hammen, 1998; Hooghiemstra et al., 2006; van der Hammen, 1989, 1995, 2003; van der Hammen & Hooghiemstra, 2000; van der Hammen et al., 1973; Wijninga, 1996). Nonetheless, when the extant páramo originated is still an open question.

The cool-mode climate of today, which emerged 2.6 my ago at the onset of the Pleistocene, is fundamentally different from the warm-mode, pre-Pleistocene climates (Fedorov et al., 2013). Four major characteristics define our modern climate: a permanent and extensive ice-cap at the North Pole, CO<sub>2</sub> levels below 200 ppm, a steep latitudinal temperature gradient pole-to-equator (~50 °C), and a steep longitudinal temperature gradient along the equatorial Pacific (Pagani et al., 2010). Understanding how those four components arose is fundamental to understanding our modern climate and making future predictions, yet we still lack satisfactory answers. The consequences of this major shift in climate mode are still being researched, but it seems to have greatly modified the extent and distribution of most biomes, including the expansion of savannas, páramos, and dry and xerophytic forests and the contraction of the rainforest (Jaramillo et al., 2015) (Figure 2a). One striking example of this shift is the Ware Formation in the northeastern region of the Guajira Peninsula (Figure 1). The Ware Formation is an upper Pliocene (3.4–2.78 Ma) fluvio-deltaic deposit (Hendy et al., 2015; Moreno et al., 2015) with a rich fossil record that includes sloths, cingulates, rodents, toxodontids, a procyonid, a camelid, large crocodiles, turtles, fossil wood, and a diverse fish assemblage (Aguilera et al., 2013a, 2013b, 2017; Amson et al., 2016; Cadena & Jaramillo, 2015; Carrillo et al., 2018; Carrillo et al., 2015; Forasiepi et al., 2014; Hendy et al., 2015; Jaramillo et al., 2015; Moreno-Bernal et al., 2016; Moreno et al., 2015; Pérez et al., 2017; Suárez et al., 2016), indicating that there were rivers with permanent water derived from local precipitation (Pérez-Consuegra et al., 2018); this is a stark contrast with the desertic environment of that region today. These profound changes, however, were not limited to terrestrial environments. The world's oceans, too, experienced a major extinction of marine megafauna at the onset of the Pleistocene (Pimiento et al., 2017).

The last large change in the history of the Neotropics occurred during the late Neogene with the terrestrial connection of Central America with South America across the Isthmus of

Panamá, which facilitated a large-scale interchange of biota across the Americas, often known as GABI (the Great American Biotic Interchange) (MacFadden, 2006a; Simpson, 1983; Webb, 1976, 1978, 1994, 1995, 2006; Woodburne, 2010). Many studies have used 3.5 Ma as the a priori date for this event (Bacon et al., 2015a), although several genetic studies of taxa with low dispersal capabilities, including bees (Roubik & Camargo, 2011), tree frogs (Pinto-Sánchez et al., 2012), salamanders (Elmer et al., 2013), freshwater *Poecilia* fishes (Alda et al., 2013), and *Amazilia* hummingbirds (Ornelas et al., 2013), among many others, have reported evidence of earlier exchanges. A recent meta-analysis across a broad range of taxa, both marine and terrestrial, indicated a large increase in the rate of migrations/vicariance migration starting at 10 Ma, rather than at 3.5 Ma as was often assumed (Bacon et al., 2015a, b; Jaramillo, 2018; Jaramillo et al., 2017a). The fossil record of Panamá indicates a similar pattern in plants (Cody et al., 2010; Graham, 1988a, 1988b, 1991, 1992, 1999, 2010, 2011; Herrera et al., 2010, 2014a, 2014c; Jaramillo et al., 2014b; Jud et al., 2016; Rodríguez-Reyes et al., 2014, 2017a, 2017b) and vertebrates other than mammals (Cadena et al., 2012b; Hastings et al., 2013; Head et al., 2012; Scheyer et al., 2013). Panamanian mammals of the early – middle Miocene in contrast are dominated by North American lineages including camels, horses, peccaries, bear-dogs, anthracotheriums, rhinocerids, geomysoid rodents, dogs, oreodonts, and protoceratids (MacFadden, 2006a, 2006b, 2009; MacFadden & Higgins, 2004; MacFadden et al., 2010, 2012; Rincon et al., 2012, 2013; Slaughter, 1981; Whitmore & Stewart, 1965); there are only two South American lineages, a monkey (Bloch et al., 2016) and a bat. Recently O’Dea et al. (2016) proposed that findings of a Miocene closure of the Central American Seaway were unsupported and provided a new age for the formation of the Isthmus at 2.8 Ma. However, both conclusions have been rejected (Jaramillo et al., 2017a; Molnar, 2017).

Most of what is written about GABI in the paleontological literature is derived from the mammal fossil record. Therefore, the mammal-derived GABI has been accepted as the de facto pattern for all other organisms, even though mammals represent only ~0.02% of all species in the Americas. Both the fossil and genetic records show that mammal exchange starts at 10 Ma and accelerates greatly at ca. 2.5 Ma rather than at 3.5 Ma (Bacon et al., 2015a; Carrillo et al., 2015; Forasiepi et al., 2014; Jaramillo, 2018; Leite et al., 2014; Webb, 1976, 2006; Woodburne, 2010). The timing for the onset of massive GABI mammal migrations has been used to suggest that factors other than a land connection drove GABI, mainly the onset of the Pleistocene cool-climate mode and all the changes that produced in the hydrological patterns of the Americas as it was discussed above (Bacon et al., 2016; Leigh et al., 2013; Molnar, 2008; Smith et al., 2012; Webb, 1976, 1978, 2006).

The development of extant Neotropical biomes has been affected by a series of historical accidents, climate changes,

and tectonic processes, many of which are still unknown. They are, however, important if we are going to be able to predict how biomes will respond to the ongoing rapid perturbations of our climate.

## Acknowledgments

Thanks to Felipe HINOJOSA and Alex CORREA–METRIO for reviewing the manuscript. Our studies have been sponsored by a number of funds and institutions including the Smithsonian Institution, Dr. David COFRIN, Anders Foundation, Fund 1923, Gregory D. and Jennifer WALSTON JOHNSON, Instituto Colombiano del Petróleo–Ecopetrol S.A., University of Florida, Missouri University of Science and Technology, Fondo para la Investigación de la Ciencia y la Tecnología del Banco de la República, USA National Science Foundation, Carbones del Cerrejón LLC., Isagén, Mark Tupper, National Geographic Society, Smithsonian Women’s Committee, Agencia Nacional de Hidrocarburos, Servicio Geológico Colombiano, Colciencias, University of Zurich, and the Corporación Geológica Ares. Thanks to the PADILLA brothers and the Centro de Investigaciones Paleontológicas, Milton RUEDA and Paleoflora, and Carlos ROSERO. Thanks to the communities of la Victoria, Warpana, Patajau, Aulechit, Nazareth, Wososopo, Sillamana, Paraguachon, La Flor de la Guajira, and Ipapura for their support and knowledge. Thanks to Fernando ETAYO, Tomás VILLAMIL, Francisca OBOH–IKUENOBE, David DILCHER, and Scott WING for their training. Thanks to Natasha ATKINS and Camilo JARAMILLO for editing. Special thanks to M.I. BARRETO for her guidance and ideas, which have been critical to all our research over the past 25 years. This contribution is an updated and modified version of a contribution to the journal of ACCEFYN in 2012.

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## Explanation of Acronyms, Abbreviations, and Symbols:

CAM	Crassulacean acid metabolism	MMCO	Middle Miocene climatic optimum
DNA	Deoxyribonucleic acid	PETM	Paleocene Eocene Thermal Maximum
ETM	Eocene Thermal Maximum	WUE	Water use efficiency
GABI	Great American Biotic Interchange	WWF	World Wildlife Fund
ITCZ	Intertropical convergence zone		

## Author's Biographical Notes



**Carlos JARAMILLO** investigates the causes, patterns, and processes of tropical biodiversity at diverse temporal and spatial scales, as well as the evolution of tropical landscapes over geological time. He intends to address questions from a paleontological perspective (mainly using fossil pollen, spores and dinoflagellates), a point of view that is vital for understanding and predicting the behavior of biota in tropical ecosystems. He is also interested in energy exploration, Cretaceous – Cenozoic biostratigraphy of low latitudes, developing methods for high-resolution biostratigraphy and the paleobiogeography of Tethys.

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