

Global Warming and Neotropical Rainforests: A Historical Perspective

Carlos Jaramillo and Andrés Cárdenas

Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Ancón, República de Panamá; email: jaramilloc@si.edu, alc1006@gmail.com

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Abstract

There is concern over the future of the tropical rainforest (TRF) in the face of global warming. Will TRFs collapse? The fossil record can inform us about that. Our compilation of 5,998 empirical estimates of temperature over the past 120 Ma indicates that tropics have warmed as much as 7°C during both the mid-Cretaceous and the Paleogene. We analyzed the paleobotanical record of South America during the Paleogene and found that the TRF did not expand toward temperate latitudes during global warm events, even though temperatures were appropriate for doing so, suggesting that solar insolation can be a constraint on the distribution of the tropical biome. Rather, a novel biome, adapted to temperate latitudes with warm winters, developed south of the tropical zone. The TRF did not collapse during past warmings; on the contrary, its diversity increased. The increase in temperature seems to be a major driver in promoting diversity.

INTRODUCTION

Why are the tropics so species rich? Why are rainforests multistratified? How do the tropical rainforest (TRF) and climate interact; specifically, how does the TRF respond to global warming events? This set of questions has been studied for a long time, and in the face of the current anthropogenic climate change they are especially relevant today. Because the generation of species occurs over geological timescales, we can use both the fossil record and DNA of extant taxa to understand changes in the diversity dynamics (through the combination of origination and extinction), floristic composition, and forest structure of the TRFs and how they relate to climate change. In this review, we focus mainly on the fossil record and how it can inform us about the history of the Neotropical rainforests. (Here, Neotropical refers to the TRFs of South America.)

The Neotropical rainforest is the most speciose biome on the planet, with more than 90,000 species of angiosperms (flowering plants) (Thomas 1999). Numerous hypotheses have been proposed to explain (a) how such great diversity was produced and (b) how it is maintained. Examination of the first issue has focused mainly on understanding the latitudinal diversity gradient (LDG), the observation that tropical biomes hold far more species than temperate ones. The LDG pattern has been the subject of many studies over the past 200 years (Willig et al. 2003). Apart from being a pervasive pattern—both terrestrial and marine realms show an increase in diversity from temperate to tropical latitudes—the LDG occurs at spatial scales ranging from local to continental (Rosenzweig 1995, Roy et al. 2000). In plants, this gradient is seen not only at the species level (Gentry 1988) but also at the generic and familial levels (Francis & Currie 2003). This is mainly because the numbers of genera and families are proportional to the number of species in a plant community (Enquist et al. 2002).

There is no consensus on the causal mechanism for the gradient, and many hypotheses have been proposed (Evans et al. 2005, Mittelbach et al. 2007, Willig et al. 2003). Most of them are based on the idea that diversity correlates with energy input (Evans et al. 2005, Willig et al. 2003). Evans et al. (2005) summarize eight proposed mechanisms to link higher energy with higher diversity, but there is no conclusive evidence for any of them. Two mechanisms often cited are the energy-supply (Wright 1983) and the evolutionary-speed hypotheses (Rohde 1992). The energy-supply hypothesis holds that diversity depends on the amount of insolation at Earth's surface (Roy et al. 1998, Wright 1983, Wright et al. 1993). The evolutionary-speed hypothesis states that rates of speciation and molecular evolution are higher in the tropics than at higher latitudes because at low latitudes, the higher temperatures increase metabolic rates and, in turn, increase mutation rates (Rohde 1992, Wright et al. 2006). Wright et al. (2006) and Allen et al. (2006) recently found genetic evidence supporting this hypothesis, although evidence to the contrary has also been produced (Bromham & Cardillo 2003). Some also contend that because speciation is a response to niche opportunities (Leigh et al. 2004), the LDG could result from the tropics having more habitats or more opportunities per habitat. This idea, however, has not been tested.

Are the tropics a cradle or a museum of diversity (Stebbins 1974)? Was the generation of the LDG a rapid phenomenon, or is it the result of a long evolutionary process? If tropics have lower rates of extinction than temperate latitudes (Stebbins 1974), one would expect that the LDG was built slowly, over tens of millions of years. If, however, rates of origination in the tropics are higher (Rohde 1992, Terborgh 1973), then the gradient should have developed over short geological times. Very few studies have tested empirically both scenarios, because doing so requires an extensive fossil record across latitudes over long periods of time. Data from marine mollusks indicate that tropical regions have been a major source of evolutionary novelty rather than a refuge (Jablonski 1993). Whether this applies to TRFs is still open to discussion.

How diversity is maintained is a different but potentially related issue. A review by Leigh et al. (2004) produced an excellent summary of the many hypotheses that have been produced to explain how numerous species can coexist. The abundance of any given species is variable, because a species faces trade-offs (MacArthur 1961); therefore, it may be abundant in a favorable niche, but rare in a nonfavorable one. Pest pressure (from pathogens and insects) is likewise variable, because pests face trade-offs in the plants they can consume. A pest has greater potential to become more specialized if the host is abundant rather than rare. Therefore, pest pressure is greater when plants of the same species are close together (as some pests specialize in abundant species), thus limiting how abundant a species can become. In short, the mechanism that maintains diversity is the antagonism by pest pressure among plants of the same species, the so-called Janzen-Connell hypothesis (Connell 1971, Janzen 1970, Leigh et al. 2004). Many experiments in the past decade have proven this mechanism (Comita et al. 2010, Johnson et al. 2012, Mangan et al. 2010). Pest pressure is supposedly more intense in the tropics because neither winters nor long dry seasons keep pest populations in check, and this could account for the LDG in tree diversity (Leigh et al. 2004). Johnson et al. (2012) demonstrated in a recent study that tree diversity in North America increases when conspecific negative density dependence is stronger and that in turn is driven by pest pressure. Recent analyses, however, have shown that seed predation is not more intense in the tropics (Moles & Westoby 2003) and that tropical plants do not have higher levels of resistance traits than plants from higher latitudes (Moles et al. 2011). Therefore, the role of pest pressure in producing the LDG is still uncertain. Perhaps the LDG results from a combination of a diversity-triggering mechanism(s) (e.g., the energy-supply and evolutionary-speed hypotheses) and a diversity-maintaining process (e.g., the Janzen-Connell effect).

DEFINING A TROPICAL RAINFOREST

What do we mean by a Neotropical rainforest? We follow the definition of Burnham & Johnson (2004), that is, a particular combination of climatic parameters, floristic composition, forest structure, and plant physiognomy. A Neotropical rainforest is a lowland forest that has high mean annual precipitation (MAP) (>1.8 m year⁻¹), high mean annual temperature (MAT) ($>18^{\circ}\text{C}$), small seasonal variation in temperature ($<7^{\circ}\text{C}$), and is dominated in abundance and diversity by angiosperms. Major families (from most to least important) are Fabaceae, Moraceae, Annonaceae, Euphorbiaceae, Lauraceae, Sapotaceae, Myristicaceae, and Arecaceae, together representing $\sim 50\%$ of species; Fabaceae, Arecaceae, Rubiaceae, Violaceae, Euphorbiaceae, Meliaceae, Sapotaceae, and Moraceae account for $\sim 60\%$ of all stems in a given hectare. The forest is multistratified, with an angiosperm-dominated closed canopy; lianas and epiphytes; and many tree species with large leaves (*mesophyllous*, $>4,500$ mm²), entire margins, and drip tips (Burnham & Johnson 2004). A compilation of data on MAP and MAT for diverse plots of tropical biomes around the world [Figure 1a,b; see also Supplemental Appendix 1 (follow the Supplemental Materials link in the online version of this article or at <http://www.annualreviews.org>)] indicates that most TRFs worldwide are between 23 and 28°C (Figure 1a), and that precipitation plays a major role in defining tropical biomes (Figure 1b). As the MAP decreases, TRFs become tropical dry forests, then tropical savannas, and ultimately deserts.

We also review the variation in climatic parameters across South America. Seventy-five percent of the landmass of South America (1.32×10^7 km²) lies within the tropical latitudinal zone (between the tropics of Cancer and Capricorn, $\sim 23.5^{\circ}$); the remaining 25% occupies temperate zones with latitudes of 23.5–60°S (Figure 1c). All landmasses in the tropical band and none of the temperate regions have MATs $>18^{\circ}\text{C}$. Although 78% of the land area in South

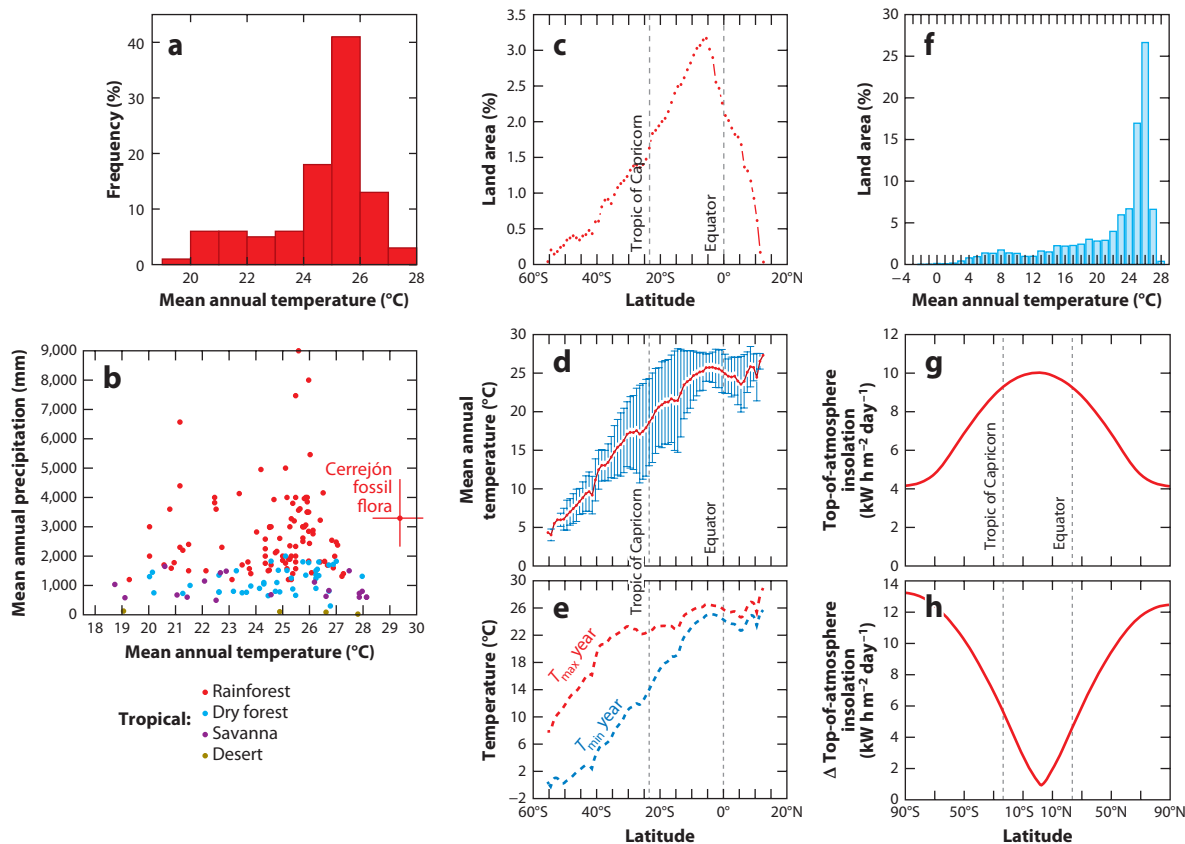


Figure 1

South American climate and tropical biomes. Source of data is found in **Supplemental Appendix 1** (follow the **Supplemental Materials link** in the online version of this article or at <http://www.annualreviews.org>). (a) Histogram showing the mean annual temperature (MAT) of 99 vegetation plots from tropical rainforests (TRFs) around the world. Most TRFs are found between 24 and 27°C, and there are no TRFs at temperatures above 29°C. (b) Mean annual precipitation (MAP) and MAT for 170 vegetation plots, including four types of tropical biomes (TRFs, dry forests, savannas, and deserts). In the tropical band, the amount of precipitation determines the type of biome; precipitation is highest in TRFs, lower in dry forests, even lower in savannas, and lowest in deserts. The Cerrejón Formation, the Paleocene fossil site in Colombia, does not have a modern analog for MAT. The error bars for the estimates of precipitation (Wing et al. 2009) and temperature (Head et al. 2009b) in Cerrejón are shown. (c) Proportion of South American land area across latitudes. A large proportion of South America is within the tropical band. (d) MAT of South America across latitudes. MAT decreases rapidly outside the tropical band, underscoring the large modern gradient of latitudinal MAT. (e) Variation between the maximum and minimum temperatures along the year across latitudes. Temperature changes drastically along the year outside the tropics, whereas the variation is minimal in the tropics. (f) Histogram showing the proportion of land area with a given MAT; a large proportion has temperatures of 24–27°C. (g) Year-long average for daily solar insolation at the top of the atmosphere across latitudes. Insolation drops rapidly outside the tropical band. (h) Differences between maximum and minimum insolation throughout the year versus latitude. Outside the tropics, the variation in insolation throughout the year is drastic.

America (1.39×10^7 km²) experiences tropical temperatures (MAT >18°C), most of that area (66.8%, 1.19×10^7 km²) falls within a MAT range of 22–27°C, underscoring that in most of the tropical zone, the range of variation in MAT is small (**Figure 1d**). Only 0.4% of the land area has a MAT of 28°C, and there are no areas with MATs >29°C (**Figure 1f**). For the rest of South America (22%), the MAT ranges from 18 to –2°C. Annual temperature variation in the tropical

band is minimal ($<5.9^{\circ}\text{C}$) and even lower ($<2^{\circ}\text{C}$) between latitudes 10°N and 10°S ; in contrast, variation at temperate latitudes can reach up to 16°C (**Figure 1e**).

Using this definition, let us review how the TRF has responded to major climatic events. As angiosperms dominate the Neotropics today (more than 90% of tropical plant species are angiosperms), a natural point at which to start this review is the Paleocene, the epoch in which the oldest known Neotropical rainforest is observed (Wing et al. 2009). There was an almost complete turnover of Neotropical ecosystems from the Cretaceous to the Paleocene: The landscape went from being completely dominated by gymnosperms and ferns in the early Cretaceous (Crane & Lidgard 1989) to completely dominated by angiosperms in the Paleocene (Jaramillo et al. 2006, Wing et al. 2009).

Our review is restricted to South America because, for the following reasons, it is uniquely suited to understanding TRF-climate interactions: (a) It is a large continent that has both tropical and temperate latitudes; (b) it has not shifted significantly in latitude since the Cretaceous; (c) it has been largely isolated since the Late Cretaceous; (d) it has had terrestrial environments since the Early Cretaceous at both temperate and tropical latitudes; (e) it lacks latitudinally oriented mountain ranges that could act as geographical barriers to biome migrations; (f) it has numerous Cretaceous and Cenozoic sedimentary basins across all latitudes with good fossil records; and lastly, (g) it has published paleobotanical literature on both temperate and tropical regions.

BIOMES OF SOUTH AMERICA

To understand the history of and prognosis for the TRF, we need to consider other biomes from both tropical and temperate latitudes as well. Although there are many classifications for the vegetation types in South America (Graham 2010), Dorman & Sellers (1989), Josse et al. (2003), and Pennington et al. (2006) identify six major groups on the basis of their broad physiognomy (e.g., trees versus herbaceous habits) (**Figure 2a**):

1. Neotropical rainforest/TRF (broadleaf evergreens): found in Amazonia and the Guianas.
2. Seasonally dry forest (broadleaf-deciduous trees): includes Caatinga, Pacific equatorial dry forests, and Chaco; it is a tree-dominated ecosystem, mostly deciduous during the dry season, with a continuous or almost continuous canopy and a ground layer in which grasses are a minor element; rainfall is $<1,600$ mm year⁻¹ and <100 mm for 5–6 months of the year (Pennington et al. 2006).
3. Broadleaf and needleleaf trees (mixed forests): include the moist Pacific temperate and the Atlantic forests, which have a mixture of angiosperms and gymnosperms, mostly evergreens.
4. Savanna/grassland/steppe: includes Orinoquia, Cerrado, Pampas, Patagonia, and Mediterranean Chile.
5. Desert.
6. Andean vegetation: includes premontane, cloud forest, and páramo/alpine vegetation.

Neotropical rainforests/TRFs occupy 36% of the land area of South America; seasonally dry forests, 14.3%; mixed forests, 9.4%; savannas/grasslands/steppes, 29.4%; Andean forests, 9.4%; and deserts, 1.5% (**Figure 2b**). Biomes adapted to drier habitats (savannas/grasslands/steppes and seasonally dry forests) are found at both temperate and tropical latitudes, although they are floristically and physiologically different from each other in the two regions. Tropical savannas and tropical dry forests are found at both ends of the TRF distribution (**Figure 2a,b**). Mixed forests are mostly found in temperate latitudes.

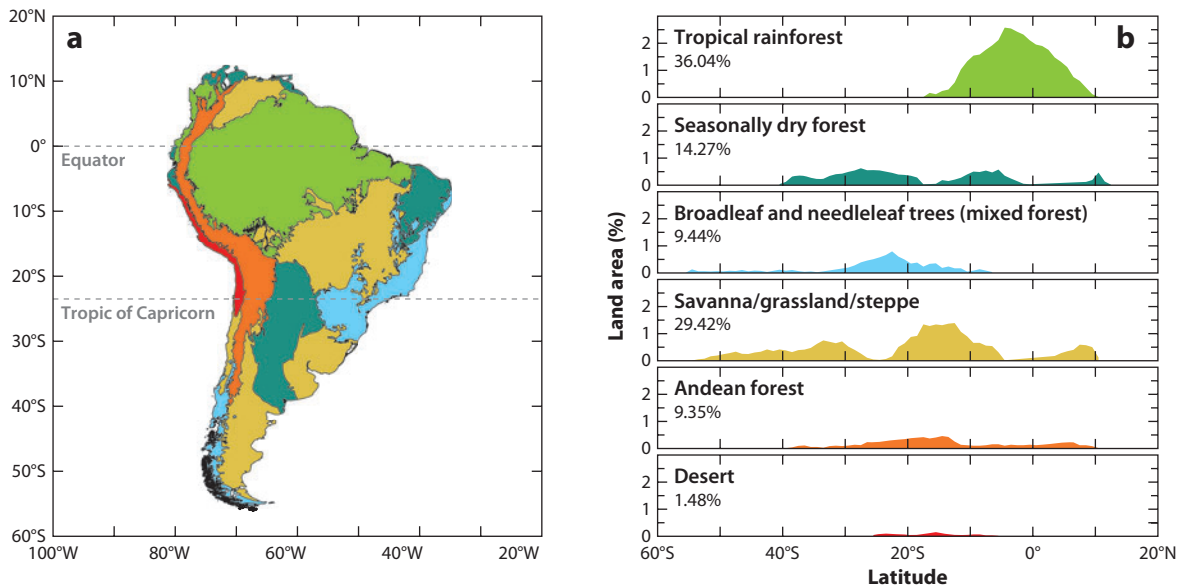


Figure 2

Principal extant biomes of South America and the land area they occupy. (a) Geographic distribution of the major biomes (after Dorman & Sellers 1989, Graham 2010, Josse et al. 2003, Pennington et al. 2006). (b) Land area coverage of each biome along its latitude. Tropical rainforests occupy 36%, whereas drier habitats (savannas and dry forests) occupy ~43%. Rainforests are bounded north and south by drier tropical habitats.

TROPICAL TEMPERATURE DURING GLOBAL WARMINGS: ARE THE TROPICS CLIMATICALLY STABLE?

For many years, $\delta^{18}\text{O}$ measured in planktonic foraminifera, a proxy for paleotemperature, indicated that surface waters from the tropics did not warm during global warming intervals as did those of the Cretaceous or the Paleogene, the so-called cool-tropic paradox (D'Hondt & Arthur 1996). Sexton et al. 2006 later found that most of the tropical planktonic foraminifera that had been analyzed had been diagenetically altered and that the diagenetic alteration—often happening near the seafloor—was producing a bias toward cooler temperatures. New estimation on pristine tropical planktonic foraminifera (called glossy) found to produce warmer temperatures than diagenetically altered foraminifera (Pearson et al. 2001) showed that the tropics indeed warm during periods of global warming.

Over the past 15 years, several additional methods for estimating temperature based on geochemistry and morphology have been developed and applied to tropical latitudes. These include terrestrial proxies such as leaf margin analysis (Peppe et al. 2011) and the snake paleothermometer (Head et al. 2009a,b), as well as marine proxies such as Mg/Ca (Hastings et al. 1998, Tripathi et al. 2003), TEX_{86} (Schouten et al. 2007), and the oxygen isotope composition of fossil fish teeth (Pucéat et al. 2007). Because many of these proxies are relatively new, the equations that related the proxy empirical value with MAT, such as the calibration equation used for TEX_{86} , have changed over time (Kim et al. 2008, 2010; Liu et al. 2009). Older estimations, therefore, need to be reevaluated. To provide an up-to-date summary of the temperature estimations for the tropics since the Cretaceous, we produced a database of 5,998 data points derived from all the publications that we are aware of that have empirical determinations of paleotemperature within tropical latitudes for both land and sea surface (see **Supplemental Appendix 2** or

<http://biogeodb.stri.si.edu/jaramillo/paleotemperature> for details). We also considered the $\delta^{18}\text{O}$ benthic foraminifera record, a proxy for deep-sea temperature, using a previous compilation of literature for both the Cenozoic (Zachos et al. 2001) and the Cretaceous (Friedrich et al. 2012). Unlike planktonic foraminifera, benthic foraminifera are not affected heavily by diagenesis, and they are a good proxy for the long-term paleoclimate (Pearson et al. 2001),

Our compilation indicates that, overall, tropical surface paleotemperatures track with global deep-sea paleotemperatures (compare panels *a* and *d* in **Supplemental Figure 1**); during global warming events, the tropical latitudes warm as well. Throughout the Cretaceous (~125–65.5 Mya), average paleotropical sea surface temperatures (32.4°C) exceeded the current maximum MAT values of the tropical sea surface (~28°C), especially during the Cenomanian-Turonian interval that reached 40°C (**Supplemental Figures 1a** and **2**; see also **Supplemental Appendix 2**). During the early Paleogene, tropical temperatures also were higher than modern values, averaging 30°C (**Supplemental Figures 1a** and **2**). There is a large gap in data for the Miocene interval (~23–5 Mya). We divided our analysis into two latitudinal bands, from 10°N to 10°S (TS0-10), and from 23.5 to 10°, both N and S (TS10-23) (**Supplemental Figure 1b,c**), as the MAT is slightly cooler in the latter (**Figure 1d**; see also Figure A of **Supplemental Appendix 2**). For TS0-10, temperatures during the largest warming events of the Cenozoic Paleocene-Eocene Thermal Maximum (PETM) and the early/middle Eocene reached ~34°C (**Supplemental Figure 1b**); the MAT reached ~32°C for TS10-23 (**Supplemental Figure 1c**).

TROPICAL AREA EXPANSION: DO TROPICAL BIOMES EXPAND DURING GLOBAL WARMINGS?

Quantifying the area available for a tropical biome is important. There is a good correlation between area and number of species, the species-area relationship (Rosenzweig 1995). As the area available for a biome increases, its total diversity increases. This pattern is also seen at a local scale. Local tree diversity is higher in regions with high tree diversity (Ricklefs 2004). Therefore, local diversity is tied to the long-term changes in the area available for a particular biome. Fine et al. (2008) explored the geographic area hypothesis, which states that larger areas should promote speciation and reduce extinction and therefore contain more species than smaller areas. They found that differences in total biome area integrated over time correlate with differences in species richness among biomes. They proposed that tropics are more diverse than temperate regions because during the Cenozoic the tropical biome area was larger than temperate biomes. They concluded that during the Eocene, for example, a tropical biome covered all of Africa and almost all of South America. Fine et al. (2008) based their study on the most accepted paleoecological models, which indicate a massive expansion of the tropical biome during global warming times in the Paleocene and an even more extreme expansion during the Eocene (Fine & Ree 2006, Fine et al. 2008, Frakes et al. 1992, Morley 2000, Scotese 2003, Wolfe 1985).

We quantified the area that would have experienced tropical temperatures (here we assign all regions with MATs >18°C as tropical) during the Early Eocene Climatic Optimum, the largest and longest warming event of the Cenozoic (**Figure 2**). To do that, we calculated the amount of land area with a MAT of 17°C, which would have been added to the tropical zone (>18°C) if the temperature had increased by 1°C. Then, we performed the same analysis but assumed a 2–10°C warming (**Figure 3a**). The resulting gradient is the rate of tropical expansion as global warming progresses, under the modern temperature gradient. We performed the same analysis under Paleocene conditions (different position of the South American plate and a flatter temperature gradient). Because the South American tectonic plate has moved north since Paleocene times (~65.5–55.8 Mya), we performed the analysis using the position of the plate for the Paleocene as reconstructed by

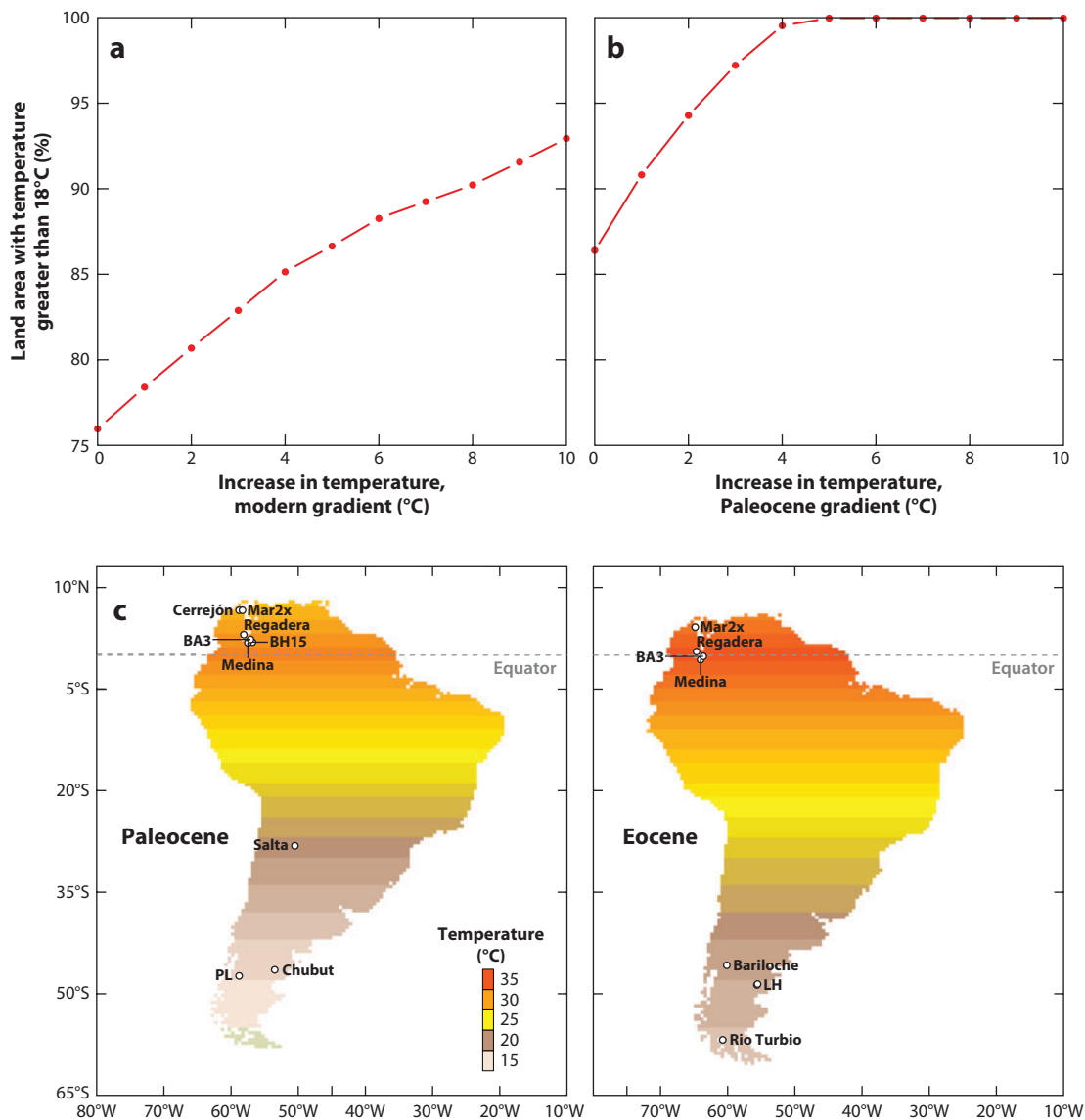


Figure 3

Model of temperature increases during the Eocene. (a) South American land area with mean annual temperatures (MATs) above 18°C as temperature increases, assuming the modern latitudinal temperature gradient. (b) Same as panel a but assuming the Paleocene's latitudinal temperature gradient. See **Supplemental Appendix 3** for calculation of the gradient (follow the **Supplemental Materials link** in the online version of this article or at <http://www.annualreviews.org>). Even a 5°C warming during the Paleocene would have resulted in all land areas of South America having MATs greater than 18°C. (c) Sites used in the floristic (pollen and megafloora) comparative analysis (see **Supplemental Appendix 4**). The temperatures are derived from the latitudinal temperature gradient calculated here for the Paleocene. Eocene temperatures are modeled after a 3°C increase relative to Paleocene temperatures. Note the absence of data in midpaleolatitudes. Tectonic plate positions are reconstructed by G-Plates. Abbreviations: LH, Laguna del Hunco/Pichileufu; PL, Palacio de Los Loros.

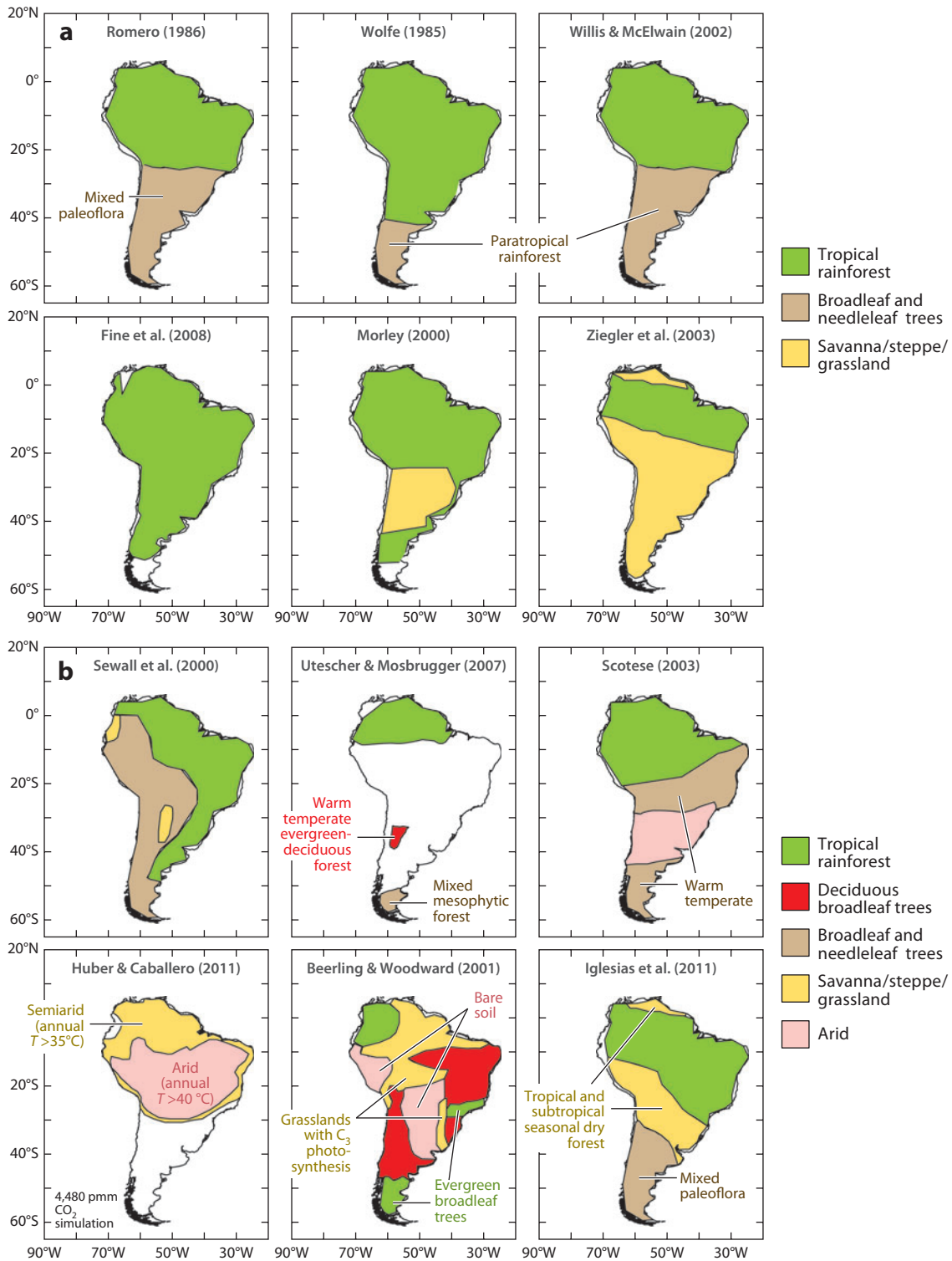
G-Plates (Boyden et al. 2011). Then, we calculated a temperature gradient for the Paleocene derived from published empirical estimates [$\text{MAT} = 31.8 - 0.52|\text{latitude}| + 0.004|\text{latitude}|^2$, $r^2 = 0.69$, $p < 0.001$, $df = 32$; see **Supplemental Appendix 3**] and quantified the expansion of tropical area that would have occurred during the 3–5°C tropical warming of the Early Eocene Climatic Optimum (Jaramillo et al. 2010; Zachos et al. 2001, 2003) (**Figure 3b**).

Assuming today's gradient, if temperatures increase 3°C, the tropics would expand by 6.7% (1.19×10^{12} km²), thus encompassing 84.7% of South America (**Figure 3a**). In contrast, during the Paleocene ~86% of South America had a MAT >18°C, but because the latitudinal temperature gradient of a warmer climate is much flatter, an increase of 3°C would have expanded the tropics to more than 97% of South America's land area (**Figure 3b,c**); with a 5°C increase, the entire continent would have experienced tropical temperatures.

The tropical area obtained here is similar to the predictions of global circulation models for South America using high levels of CO₂ (2,240–4,480 ppm) (Huber & Caballero 2011), as well as several paleoecological models (Fine & Ree 2006, Fine et al. 2008, Frakes et al. 1992, Morley 2000, Scotese 2003, Wolfe 1985, Ziegler et al. 2003) indicating a large expansion of tropical biomes during the early Eocene (**Figure 4**).

We analyzed South America's plant fossil record of the Paleocene and Eocene, to test the hypothesized expansion of tropical biomes during global warming. We compared the floristic composition of both palynological and megafossil records of tropical sites (Colombia/Venezuela) with that of temperate sites (Argentina) to assess their degree of similarity. Abundance data are ideal to produce such a comparison, and pollen count data are available for the published record of the tropics (e.g., Jaramillo et al. 2006, 2010; Jaramillo 2002; Jaramillo & Dilcher 2001); however, they are not available for most of the published palynological records of Argentina for the Paleocene-Eocene interval (Archangelsky 1973; Archangelsky & Romero 1974; Archangelsky & Zamalao 1986; Báez et al. 1990; Melendi et al. 2003; Menéndez & Caccavari de Filice 1975; Romero 1977; Romero & Castro 1986; Romero & Zamalao 1985; Volkheimer et al. 2006, 2007). Therefore, we based our comparison on presence/absence data only. We provided species lists for six Paleocene and four Eocene sites from the Neotropics and two Paleocene and two Eocene sites from Argentina (**Figure 3c**; see also **Supplemental Appendix 4**). Very few Argentinian studies provide the precise stratigraphic position of samples; rather, most papers present a list of the species that were found in a given geological formation. To make the Neotropical quantitative data as similar as possible to the Argentinian data, we produced a list for each locality of the species of Paleocene and/or Eocene age by pooling the species list of all samples into a single sample, excluding singletons (species that only appeared in one sample). Rare species, mostly unnamed, could enhance the differences among sites and introduce noise in a similarity analysis, especially when using presence/absence data and calculating the Jaccard index (see below) (Chao et al. 2006). We used a total of 360 samples for the Paleocene sites (Cerrejón = 181 samples, BA3 = 40, Regadera = 19, Mar2x = 73, BAH = 30, Medina = 17) and 163 samples for the Eocene sites (BA3 = 38 samples, Regadera = 21, Mar2x = 92, Medina = 12) in the Neotropics.

To compare the similarity among sites, we calculate the Jaccard index, $\text{JI} = 2Z / (1 + Z)$, where Z is $(A + B - J) / (A + B)$ and A is the number of species in site A , B is the number of species in site B , and J is the number of species that occur in both sites (Magurran 2004). The index ranges from 0 (identical sites) to 1 (completely different) and is appropriate for calculating presence/absence data (Magurran 2004). Although the index produces biased results when sample sizes are small or species richness is large [e.g., when comparing two sites that contain numerous rare species (Chao et al. 2006)], the lack of abundance data restricts our analysis to presence/absence data. All analyses were done using R for statistical computing and the package Vegan (Oksanen et al. 2010, R Dev. Core Team 2012; see **Supplemental Appendix 4** for a discussion the code used).



Paleocene

The difference in floristic composition between the Neotropical sites and the temperate South American sites is striking (**Table 1, Figure 3c**), during the Paleocene and, even more, during the Eocene. The mean JI among Paleocene tropical sites is 0.83 (SD = 0.1, N = 15). The JI between the two Argentinian sites is 0.94 (N = 1). The mean JI between tropical and Argentinian sites is much higher at 0.98 (SD = 0.01, N = 12) and significantly different from the among-tropical JI mean (t-test, $p < 0.001$, $df = 14.3$). In other words, the Neotropical floras are more similar to each other than to those in the Argentinian sites, and the number of shared elements between Neotropical and Argentinian sites is minimal. The total number of species in Paleocene tropical sites is 547, whereas in Argentinian localities it is 163. The total number of species shared between the Neotropics and Argentina is 12. The mean number of shared species among tropical sites is 38, whereas it is 4.2 between Argentinian and tropical sites (**Table 1**), and the difference is significant (t-test, $p < 0.001$, $df = 14.7$).

The species shared by temperate and tropical sites can be grouped into three categories: (a) those species that are common in the Neotropics during the Paleocene but rare in Argentina, i.e., *Longapertites* sp. (Arecaceae), *Proxapertites operculatus* (Araceae), *Proxapertites* sp. (Araceae), and *Spinizonocolpites* sp. (Arecaceae, a mangrove taxa); (b) those that are common in Argentina but very rare in the Neotropics, i.e., *Proteacidites* spp. (Proteaceae) and *Araucariacites* spp. (Araucariaceae); and (c) those that can be common in both regions, i.e., *Ulmoideipites krempii* (Ulmaceae) only. Five additional morphotypes are nondescriptive morphologies that are commonly found everywhere: *Matonisorites* sp. (fern), *Polyodiaceosporites* sp. (fern), *Rugulatisporites* sp. (fern), *Psilatricolporites* sp., and *Rousea* sp.

Eocene

We would expect greater similarity between tropical and temperate sites in the Eocene as temperature increases; however, results indicate otherwise. The mean JI among Eocene tropical sites is 0.80 (SD = 0.07, N = 6). The JI between the two Argentinian sites is 0.85 (N = 1). The mean JI between tropical and Argentinian sites is much higher at 0.98 (SD = 0.003, N = 8) and significantly different from the among-tropical JI mean (t-test, $p < 0.001$, $df = 5.01$). The Eocene Neotropical floras are more similar to each other than to those of the Argentinian sites, and the number of shared elements between Neotropical and Argentinian sites is minimal, even lower than during the Paleocene. The total number of species in Eocene Neotropical sites is 572, 93 in Argentina, and only 2 between Neotropical sites and Argentina. The mean number of shared species among Neotropical sites is 61.5, whereas it is 0.2 between Argentinian and Neotropical sites (**Table 1**), and the difference is significant (t-test, $p < 0.001$, $df = 5.02$). Shared species include *Podocarpites* sp. (Podocarpaceae), common in Argentina but very rare in the Neotropics during the Eocene, and *Polyodiaceosporites* sp. (fern), rare in both regions.

Figure 4

Twelve different models of plant biomes for South America during the Eocene. There are great discrepancies among the models, in terms of both tropical rainforests and dry habitats. (a) Several models infer the presence of a novel temperate biome (Romero 1986), a paratropical rainforest (Willis & McElwain 2002, Wolfe 1985), the expansion of tropical rainforests toward temperate latitudes (Fine et al 2008), or the expansion of grasslands (Morley 2000, Ziegler et al. 2003). (b) Another set of models infer the presence of a more patchy distribution of a variety of biomes including grasslands and arid regions (Beerling & Woodward 2001, Huber & Caballero 2011, Iglesias et al. 2011, Scotese 2003, Sewall et al 2000). Utescher & Mosbrugger (2007) infer a tropical rainforest, a warm temperate evergreen-deciduous forest, and a mixed mesophytic forest.

Table 1 Jaccard Index and number of pollen/spore morphospecies shared for eight sites in the Paleocene of South America and six sites in the Eocene of South America^a

Paleocene															
Latitude	Longitude	Paleo-latitude	Paleo-longitude	Species/site	Site	Cerrejón	Regadera	Medina	Mar2x	BH15	BA3	Chubut			
						Jl ^b	Jl ^c	Jl	Jl	Jl	Jl	Jl	Jl	Jl	Jl
11.07	-72.69	6.5	-58.8	189	Cerrejón										
7.40	-72.40	2.9	-58.1	65	Regadera	0.87	30								
4.50	-73.10	1.7	-57.5	135	Medina	0.7	74	0.8	33						
11.06	-72.17	6.5	-58.3	289	Mar2x	0.82	74	0.91	29	0.84	58				
4.57	-72.43	1.8	-56.8	66	BH15	0.9	24	0.89	13	0.87	23	0.94	19		
4.98	-72.75	2.2	-57.1	118	BA3	0.83	45	0.92	13	0.8	43	0.92	31	0.5	61
-43.72	-67.28	-46.6	-53.5	138	Chubut	0.97	9	0.99	2	0.96	9	0.98	7	0.97	5
-25.34	-65.20	-28.3	-50.5	34	Salta	0.99	2	0.99	1	0.98	3	0.99	3	0.99	1
Eocene															
Latitude	Longitude	Paleo-latitude	Paleo-longitude	Species/site	Site	BA3	Regadera	Mar2x	Medina	Rio Turbio					
						Jl	Jl	Jl	Jl	Jl	Jl	Jl	Jl	Jl	Jl
4.98	-72.75	-0.2	-63.4	188	BA3										
7.40	-72.40	0.4	-64.4	111	Regadera	0.82	45								
11.06	-72.17	4	-64.9	331	Mar2x	0.89	53	0.86	53						
4.50	-73.10	-0.7	-63.8	184	Medina	0.76	72	0.68	72	0.83	74				
-51.60	-72.30	-56.8	-60.7	50	Rio Turbio	1	0	1	0	1	0	1	0		
-40.67	-71.08	-45.8	-60.1	63	Bariloche	1	0	1	0	0.99	2	1	0	0.85	14

^aSpecies list in **Supplemental Appendix 4** (follow the **Supplemental Materials** link in the online version of this article or at <http://www.annualreviews.org>).

^bJl, Jaccard index (presence/absence).

^cJ, number of species shared.

The analysis shows that Neotropical and Argentinian floras are even less similar to each other in the Eocene than in the Paleocene. That is opposite to what we would expect if tropical biomes expanded during the early to middle Eocene global warming, which represents the warmest time during the Cenozoic (Zachos et al. 2001).

The limited abundance data also show a similar pattern. In early Eocene Bariloche (paleolatitude 45°S) (Melendi et al. 2003), gymnosperms dominate the assemblage (32–46%), followed by angiosperms (25–33%), then ferns/bryophytes (3–4.5%). *Plicatopollis*, *Haloragacidites*, and *Proteacidites* dominate most of the angiosperms (49–83%). In middle Eocene Bariloche (paleolatitude 45°S) (Báez et al. 1990) and Rio Turbio (paleolatitude 56°S) (Romero 1977), gymnosperms (mainly *Podocarpites*) and *Nothofagidites* dominate the assemblage (>50%). In contrast, the abundance of these taxa in the Eocene Neotropics represents less than 1% of the Neotropical assemblage (see, e.g., Jaramillo et al. 2006, 2010; Jaramillo 2002; Jaramillo & Dilcher 2000, 2001; Ochoa et al. 2012; Pardo-Trujillo et al. 2003; Rodríguez-Forero et al. 2012).

Data from megafloras (e.g., leaves, fruits) are very scarce for the Neotropics. The only well-studied megaflora is that for middle to late Paleocene sites of the Cerrejón Formation in northern Colombia (Carvalho et al. 2011; Doria et al. 2008; Gomez et al. 2009; Herrera et al. 2008, 2011; Stull et al. 2012; Wing et al. 2009). Although there are abundant data from megafloras of Paleocene and Eocene southern South America, most of the published literature lacks abundance data. Only two publications have quantitative, stratigraphically controlled paleobotanical data derived from the same collection method as data for the Cerrejón floras (CF); to make the comparison more meaningful, we focus on these publications. They include middle Paleocene Palacio de Los Loros (PL; 45.9°S, 69.2°W) (Iglesias et al. 2007) and early Eocene Laguna del Hunco/Pichileufu (LH; 42.4°S, 70.03°W) (Wilf et al. 2005), both located in Argentina (**Figure 3c**).

To compare the family-level taxonomic composition of the CF, PL, and LH with that of extant TRFs, we followed the same method and dataset used by Wing et al. (2009), with the addition of the Argentinian sites. For living sites, Wing et al. used 72 of Gentry's 0.1-ha transects (Phillips et al. 2002) and tabulated the proportions of species and individuals belonging to each family. For fossils, they tabulated the proportion of leaf morphotypes in each family for the whole flora and the number of leaves per family collected in unbiased leaf censuses. We collected the same information from the raw data of PL and LH publications (Iglesias et al. 2007, Wilf et al. 2005). Wing et al. (2009) compared the similarities between all pairs of living and fossil sites by calculating the Spearman's rank-order correlation coefficient and concluded that in terms of rank-order diversity and abundance, Paleocene CF is already within the range of living TRFs. This pattern indicates that the representation of tropical families within the TRF biome during the entire Cenozoic is very conservative (Ricklefs & Renner 2012), as the most abundant families in CF are among the most abundant families in modern TRFs (Ricklefs & Renner 2012, Wing et al. 2009).

The comparison of both PL and LH floras with extant Neotropical forests indicates that Argentinian sites are significantly different. The mean Spearman coefficient for leaf abundance is 0.12 for PL versus modern sites and 0.17 for LH versus modern sites. In contrast, the mean Spearman coefficient is 0.48 among the modern sites, 0.27 for CF-conservative versus modern sites, and 0.34 for CF-best-guess versus modern sites (**Table 2**). The Spearman coefficient of living sites compared to CF is significantly different from that of living sites compared to either PL or LH (t-test, $p < 0.001$, $df = 122.8$ for LH, $df = 136.3$ for PL). Family analysis of species or leaf morphotype shows similar results. The mean Spearman coefficient of PL versus modern sites is 0.13 and 0.16 for LH versus modern sites, whereas it is 0.48 among the modern sites; it is 0.28 for CF-conservative versus modern sites and 0.37 for CF-best-guess sites (**Table 2**). The Spearman coefficient of living sites compared to CF is significantly different from that of

Table 2 Floristic comparison of the Cerrejón, Palacio de los Loros, and Laguna del Hunco/Pichileufu megafloras and extant Neotropical rainforests

	Latitude	Longitude	Paleolatitude ^a	Paleolongitude
Cerrejón (middle Paleocene)	11.07	-72.69	6.5	-58.8
Palacio de los Loros (middle Paleocene)	-45.91	-42.46122	-48.7	-55.6
Laguna del Hunco (early Eocene)	-42.46122	-70.03528	-47.5	-58.8
Comparisons using proportion of stems or leaves per family				
	Minimum	Mean	Maximum	Median
All 72 Gentry plots to one another	-0.11	0.48	0.85	0.49
Gentry plots to Cerrejón ^b (conservative)	0.1	0.27	0.38	0.27
Gentry plots to Cerrejón (best guess)	0.13	0.34	0.49	0.36
Gentry plots to Palacio de los Loros	0	0.13	0.26	0.12
Gentry plots to Laguna del Hunco/Pichileufu	0.04	0.17	0.26	0.17
Comparisons using proportion of species per family				
	Minimum	Mean	Maximum	Median
All 72 Gentry plots to one another	-0.12	0.48	0.87	0.5
Gentry plots to Cerrejón (conservative)	0.019	0.28	0.42	0.29
Gentry plots to Cerrejón (best guess)	0.08	0.37	0.55	0.4
Gentry plots to Palacio de los Loros	-0.02	0.12	0.25	0.11
Gentry plots to Laguna del Hunco/Pichileufu	-0.12	0.16	0.26	0.16

^aPaleolatitudes calculated by G-Plates for fossil sites are also provided.

^bCerrejón data indicate both conservative taxonomic affinities and best guesses.

living sites compared to either PL or LH (t-test, $p < 0.001$, $df = 120.6$ for LH, $df = 116.8$ for PL).

In summary, neither PL nor LH can be considered a TRF, as defined in this review, contrary to CF, which can be. Wilf et al. (2005) summarize the LH flora as having multilayered vegetation with canopy trees such as *Araucaria*, vines (Menispermaceae, Sapindaceae), shrubs and small trees [e.g., *Akania* (Akaniaceae), *Gymnostoma* (Casuarinaceae), "*Laurelia*" (Atherospermataceae), and "*Roupala*" (Proteaceae)], ground cover, and small-statured plants (mosses, cycads, monocots, and diverse ferns). Temperate Eocene South American floras have Neotropical elements, and some tropical taxa migrated south during Eocene global warming events, as has been documented (Hinojosa & Villagran 2005; Morley 2000; Romero 1986, 1993; Wilf et al. 2005). However, the bulk of the forest is not similar to a TRF, as our meta-analysis of both pollen and megafloras has indicated. Romero (1978, 1986, 1993) called this temperate Paleogene biome the Mixed Paleoflora, a flora that appeared during the Paleocene south of 44°S and by the middle Eocene expanded north to occupy the entire region south of ~24°S (Romero 1986). This Mixed Paleoflora was a unique ecosystem with no modern analog. It was a temperate region with a relatively warm climate, high annual precipitation, little seasonal variation (Hinojosa & Villagran 2005), and a mixture of angiosperms and gymnosperms (mainly Araucariaceae and Podocarpaceae) (Hinojosa & Villagran 2005; Romero 1978, 1986, 1993). It combined Neotropical elements, cold-temperate elements from Gondwana—sub-Antarctic in origin—and in situ Chaco forests.

The high abundance and diversity of gymnosperms (e.g., Araucariaceae, Podocarpaceae) in both LH and PL, the numerous families that are rare in the tropics but abundant in southern latitudes (e.g., Proteaceae, Myrtaceae, Casuarinaceae, Cunoniaceae, Atherospermataceae,

Akaniaceae), and the absence of typical Neotropical clades as our analysis showed (e.g., Zingiberales, Meliaceae, Anacardiaceae, Sapotaceae, Moraceae, Annonaceae, Violaceae, and only one Euphorbiaceae) suggest that TRFs did not expand during global warming events, not even during the Early Eocene Climatic Optimum. Individual lineages did migrate, but not the forest as a whole. This distinction has great implications, mainly because the evapotranspiration and photosynthetic properties of lowland Neotropical forests are different from those of other types of forests, including gymnosperm forests (Boyce & Lee 2010); therefore, a climatic model will produce very different outcomes in estimations of temperature, rainfall, and seasonality for a given region depending on the type of forest chosen. For instance, Sewall et al. (2000) demonstrated that changes in boundary conditions of modeled vegetation produce significant variations in continental-scale climate, changing land temperatures of outcome models by up to 6°C.

How does our analysis compare to biome models that have been developed for the Eocene? There is great disparity in the vegetation models that have been proposed for the early/middle Eocene interval (**Figure 4**). One group of models proposes a lack of significant arid conditions in South America (Fine et al. 2008, Romero 1986, Willis & McElwain 2002, Wolfe 1985). Romero (1986) proposed a Neotropical Paleoflora (a TRF) occupying the entire South American continent down to ~60°S by the early Paleocene, and a Mixed Paleoflora (as described above) that developed at the onset of the Paleocene in the southern tip of Argentina, expanded progressively northward during the Paleocene and early Eocene, and by the middle Eocene covered the entire region south of 24°S (**Figure 4a**). Wolfe (1985) expanded the TRF to ~40°S and inferred that southward of 40°S was a paratropical rainforest (**Figure 4a**; also see sidebar, Paratropical Rainforest). According to Wolfe, during the PETM, the TRF covered almost all of South America. Frakes et al. (1992) also used Wolfe's maps in their Eocene biome reconstructions. Wolfe's paratropical rainforest is not equivalent to the Mixed Paleoflora proposed by Romero and confirmed by our analysis, because the Mixed Paleoflora does not have a modern analog and it does not resemble a TRF. Willis & McElwain (2002) extend the TRF (named tropical everwet) to ~25°S and contend that the remainder of South America is covered by a subtropical summerwet or paratropical forest, similar to Wolfe's paratropical rainforest (**Figure 4a**). Fine et al. (2008) extend the TRF to cover almost the entire continent (**Figure 4a**).

A second set of models proposes the existence of dry habitats of different size ranges and degrees of aridity (Beerling & Woodward 2001, Iglesias et al. 2011, Morley 2000, Scotese 2003, Sewall et al. 2000, Utescher & Mosbrugger 2007, Ziegler et al. 2003). Morley (2000) extended the TRF down to the southern tip of Argentina (**Figure 4a**), called the Southern Megathermal Province. A broad dry band between 20° and 40°S around the subtropical high-pressure zones, but with a humid corridor

PARATROPICAL RAINFOREST

Wolfe (1979) denominates a paratropical rainforest as a biome with rainforest-like physiognomic characteristics, including a broadleaf evergreen forest with some broadleaf-deciduous trees and conifers as minor elements. It is composed of two closed canopies (as opposed to three in the TRF) and an emergent stratum. Its leaves are slightly smaller than those of the TRF, 60–75% of its tree species have entire margin leaves, and it has high plant diversity. Examples of paratropical rainforests can be found in some areas of Southeast Asia. Differentiating a paratropical rainforest (see Wolfe 1979) from a TRF in the fossil record seems to be difficult. Nevertheless, paratropical rainforest is a term that has been used widely in the literature of both extant and fossil floras, but it probably has multiple meanings beyond what Wolfe's original definition proposed. Therefore, it should not be used.

along the eastern coast of South America, separates this province from tropical latitudes. Ziegler et al. (2003) proposed that most of temperate and northern South America had high evaporation, with only a narrow band of tropical wet environments around 10° of the equator (**Figure 4a**). According to Sewall et al. (2000) TRFs extended into high latitudes along the eastern side of South America, and most of South America was covered by a broadleaf and needleleaf tree forest, similar to modern moist temperate forests of Argentina and Chile. There are also some pockets of savannas (**Figure 4b**). Utescher & Mosbrugger (2007) proposed a TRF biome around 10°S, a warm temperate evergreen-deciduous forest, with extratropical evergreens and deciduous taxa of high diversity between latitudes 30° and 40°S, and a mixed mesophytic forest south of 50°S (deciduous taxa, needleleaves, and evergreens) (**Figure 4b**). Scotese (2003) proposed a TRF distribution similar to modern times, with a broad band of arid environments in midlatitudes bounded south and north by warm temperate vegetation (**Figure 4b**). Huber & Caballero (2011) produced a climatic model to simulate early Eocene temperatures using high levels of atmospheric CO₂ (4,480 ppm). Their results indicate that most of the tropical region would have been above 35°C and the central Amazon should have been >40°C, suggesting a very arid to semiarid habitat for most of the Neotropics (**Figure 4b**). Iglesias et al. (2011) (**Figure 4b**) proposed a TRF extending to 30°S that was bounded by broad bands of tropical and subtropical seasonal dry vegetation extending to 40°S and a band of warm temperate vegetation, similar to Romero's Mixed Paleoflora, south of 40°S covering Patagonia entirely. Beerling & Woodward (2001) proposed extensive functional desert and savanna plant biomes (grasses with C₃ photosynthetic pathways) covering most of South America, with broadleaf evergreens restricted to the northwestern corner of South America, the Mata Atlantica region in southeast Brazil, and Patagonia. In their reconstruction there are also extensive deciduous broadleaf trees in eastern Amazonia and southwestern South America. This distribution is remarkably different from other interpretations (**Figure 4b**).

Our meta-analysis, based on empirical fossil data, diverges sharply from the biome models described above. Our analysis concluded that during the Eocene warming, TRFs did not extend into temperate regions, as was already suggested by some (Utescher & Mosbrugger 2007), nor is there evidence of increased aridity or expansion of savanna biomes (Jaramillo et al. 2006, 2010). Therefore, models (and the studies based on them) that have indicated significant latitudinal expansion of TRFs in South America need to be reevaluated (e.g., Fine & Ree 2006, Fine et al. 2008). It is also evident that a unique flora, as proposed by Romero (1978, 1986, 1993) and confirmed here, developed in midlatitudes of South America and expanded to occupy all regions south of the TRF biome as the warming of the Paleogene progressed. This forest is a mixture of angiosperm and gymnosperm trees, developed under a wet climate with warm winters, and does not have a modern analog (Hinojosa & Villagran 2005). We still do not know how this forest behaved in ecophysiological terms (e.g., evapotranspiration, photosynthesis). Is it more similar to a TRF or to a temperate forest such as the Pacific temperate forests of Chile? We need more ecophysiological studies of these extinct forests; fortunately, there is a growing number of tools available to address questions such as stomatal density, leaf venation density, and isotopes (Brodribb & Feild 2010, Diefendorf et al. 2010, Feild et al. 2011, Royer et al. 2007), and the fossil record of the Paleogene of the Americas is excellent.

Why, then, did the TRF not expand if the temperature range allowed it to (see sidebar, Tropical Savannas)? One limiting factor might have been solar insolation. Values of solar insolation at the top of Earth's atmosphere are more intense within the tropical band (below 23.5°), where Earth's surface directly faces the Sun at some point of the year (**Figure 1g**). Not only is insolation higher in the tropics, but also the variation in insolation along the year is minimal. At the equator, the annual maximum solar insolation is only 13% higher than the annual minimum, whereas outside

TROPICAL SAVANNAS

How do tropical savannas (e.g., dry belts) behave during global warmings? There are widely different interpretations of tropical dry-belt changes during times of intense global warming, such as during the Eocene or for projected future warmings (Beerling & Woodward 2001, Cox et al. 2004, Harris et al. 2008, Huber & Caballero 2011). The overall fossil record of savannas seems to indicate that savannas and dry forests extended radically over the past 15 Ma and were not a dominant element of the landscape before (Edwards et al. 2010). This broad pattern is also supported by DNA-based phylogenies of the four large groups of plants characteristic of dry habitats—Cactaceae, Agavaceae, Poaceae, and the ice plants of South Africa (Arakaki et al. 2011, Edwards et al. 2010, Majure et al. 2012)—and by phylogenetic studies of dry-biome history, such as those for the Cerrado (Simon et al. 2009). Therefore, it appears that dry belts expanded during icehouse rather than greenhouse times in Earth's history. Why are savannas not widespread during warming times? Perhaps because under high levels of CO₂ and/or reduced hydric stress, savannas cannot compete with trees (see, e.g., Higgins & Scheiter 2012). This subject needs further exploration.

the tropics, this proportion increases greatly, reaching ~400% at 50°N and S (Osborne 2000) (**Figure 1b**). These two properties would not be altered by a global warming event. Insolation can affect the metabolism of plants, because solar radiation has a large influence on the productivity and quality of plant growth. Moreover, because temperate latitudes have both lower solar radiation and higher variation in insolation throughout the year than tropical latitudes, tropical plants might be less competitive than temperate plants at temperate latitudes, regardless of temperature.

TEMPERATURE AND FOREST DIVERSITY

On the basis of the assumption that extant tropical vegetation is near to its climatic optimum, several authors have predicted that the increase in global temperature will cause tropical ecosystems to collapse (Huber 2008, Stoskopf 1981, Tewksbury et al. 2008). The fossil record of the Neotropics, in contrast, shows that biotas were able to cope with high temperatures over extensive periods of time (several millions of years). Paleocene (60 Mya) TRFs from Cerrejón, northern Colombia, were similar in composition and physiognomy to modern TRFs (Wing et al. 2009) but were ~2°C warmer than today (Head et al. 2009b, Jaramillo et al. 2010) and had higher levels of CO₂, >400 ppm (Royer 2006) (**Figure 1b**). The forest also supported a rich fauna that included large snakes, crocodiles, and giant turtles (Bloch et al. 2008; Cadena et al. 2010, 2012a,b; Cadena & Jaramillo 2006; Hasting et al. 2010, 2011; Head et al. 2009a,b). There were two subsequent intense warming events in the Cenozoic: the short, 200-ka PETM and the longer, 2–4-Ma Early Eocene Climatic Optimum, when tropical temperatures reached ~32–34°C (Jaramillo et al. 2010; Zachos et al. 2002, 2003). In both cases, there was a significant increase in tropical plant diversity (~30%) associated with the event, which resulted from the rise in origination rates and steady rates of extinction (Jaramillo et al. 2006, 2010). Moreover, most of these originations appeared to be the product of in situ speciation, rather than migration from other regions. This Eocene radiation of multiple tropical clades also can be seen in the phylogeny of some TRF elements including epiphytic ferns, orchids, and leaf-cutter ants (Ramirez et al. 2007, Schuettelpelz & Pryer 2009, Schultz & Brady 2008; also see sidebar, Climate Models for Tropical Zones During Global Warmings).

Even though recent studies of leaves from canopy trees have shown that the upper thermal limit could be as high as ~50–53°C (Krause et al. 2010), and that elevated nighttime temperature

CLIMATE MODELS FOR TROPICAL ZONES DURING GLOBAL WARMINGS

An increase in TRF diversity during Eocene warming events contrasts with paleoclimatic models that have predicted a MAT >38°C for the Neotropics producing a continental collapse of TRF (Bowen & Zachos 2010, Huber 2008, Huber & Caballero 2011). This result underscores that paleoclimatic models are still incapable of reproducing global warm climates, in which the temperature gradient between the equator and the poles is reduced to a minimum. Most climate models use an increase in CO₂ to raise the temperature in the poles (Huber & Sloan 1999, 2000; Huber et al. 2003; Shellito et al. 2003; Sloan & Barron 1992; Sloan & Morrill 1998; Sloan & Rea 1995; Sloan & Thomas 1998; Sloan et al. 1995), but at the same time, tropical temperature increases too much, above most empirical data. There must be an unknown mechanism that allows poles to increase temperature at much faster rates than the equatorial zones.

increases growth in some tropical species (Cheesman & Winter 2013), various deleterious effects can be seen in plants as temperature rises, including an increase in respiration that decreases net production, a decrease in photosynthesis, an intensification in isoprene emissions, an increase in photoinjury, and an increase in leaf stress (Bassow et al. 1994; Huber 2008, 2009; Lerda & Throop 1999; Lewis et al. 2004; Stoskopf 1981; Tewksbury et al. 2008). How, then, can we explain why during past global warming events the diversity and biomass of tropical plants increased, rather than decreased, at both short (thousands of years) and long (millions of years) geological timescales? Leaf temperature, an essential factor for plants, depends mainly on three factors: air temperature, levels of atmospheric CO₂, and soil humidity. The combination of these factors determines plant responses to an increase in ambient temperature. Paleogene global warming events are characterized by elevated levels of CO₂ (Royer 2010), high values of precipitation in most of the Neotropics (Jaramillo et al. 2010, Wing et al. 2009), and low levels of aridity (Jaramillo et al. 2010). Physiological studies indicate photosynthesis is more efficient at higher temperatures (up to 10°C) if plants are subjected to elevated levels of CO₂ and soil humidity (Aber et al. 2001, Berry & Björkman 1980, Lloyd & Farquhar 2008, Niu et al. 2008). Furthermore, the efficiency in a plant's water use can increase up to 50% when CO₂ doubles (Cernusak et al. 2011). The genetic basis of photosynthetic capability is deeply rooted in angiosperm phylogeny, suggesting that Cenozoic plants used the same tools for photosynthesis as modern plants. It is probable, then, that extant plants already possess the genetic variability needed to cope with changes in temperature and CO₂, as some authors have suggested (Lloyd & Farquhar 2008).

We have seen that TRFs can function under elevated temperatures, but why would diversity increase? Previous studies had proposed that Eocene Neotropical diversity increased because of the species-area relationship (Rosenzweig 1995) as TRF area expanded (Fine & Ree 2006, Fine et al. 2008, Jaramillo et al. 2006). However, the meta-analysis presented here indicates that TRF biomes do not expand during global warming events. Additionally, species migration from temperate latitudes could not account for an increase in diversity, as most originations appeared to be in situ (Jaramillo et al. 2010).

The increase in diversity during the PETM and early Eocene happened across all latitudes, not only in the tropics, and involved not only plants but also mammals. Plant diversity in Argentina increased (Wilf et al. 2003), and the three modern orders of mammals (Artiodactyla, Perissodactyla, and Primates) evolved within the PETM interval, in just a few hundred to a few thousand generations (Gingerich 2006). The increase in temperature per se could be the driver of the spike

in origination, as other factors related to energy (e.g., solar radiation) that have been proposed to explain high diversity—the energy-supply hypothesis (Willig et al. 2003)—would not likely have changed substantially during a global warming event.

An increase in temperature could speed up biochemical kinetics (Allen et al. 2006), which in turn would increase rates of molecular evolution (Allen et al. 2006, Rohde 1992, Wright et al. 2006). There is a significant correlation between rates of molecular evolution at plastid and nuclear loci and angiosperm species richness (Barracough & Savolainen 2001). This correlation could arise, as changes in molecular rates may lead to shorter generation times and/or faster mutation rates that in turn could lead to a greater diversity (Davies et al. 2004). However, Davies et al. (2004) demonstrated a strong relationship between molecular rates of evolution and energy, and between species richness and energy, but did not find a strong relationship between species richness and molecular rates; this relationship seems to be an artifact of both being correlated previously with energy measures.

There is no consensus yet on whether high rates of molecular evolution promote speciation (Schemske 2009). The biotic interactions hypothesis (Dobzhansky 1950) is an alternative explanation. Temperature is a critical variable for living organisms; almost every physical characteristic depends on it (e.g., average kinetic energy of molecules, circulation or conduction of fluids, rates of reaction). Therefore, a rise in temperature would increase metabolic and growth rates in an organism as well as the strength and variety of interactions among species (Vermeij 2003, 2005). Given that selection in warm environments is largely driven by biotic interactions, rather than governed by abiotic factors, and that biotic interactions are stronger in a warmer climate, the shifting selective landscape may promote speciation by creating a more intense search for a phenotypic optimum (Schemske 2009). This process, in turn, could become more efficient in promoting higher diversity as the rates of molecular evolution also are enhanced, providing the source of genetic novelties needed to increase rates of speciation.

SUMMARY POINTS

1. Tropical temperatures increase during global warming events. Temperatures rose $\sim 5\text{--}7^\circ\text{C}$ during the mid-Cretaceous and $3\text{--}5^\circ\text{C}$ during both the PETM and the Early Eocene Climatic Optimum, constituting the three largest warming events over the past 130 Ma.
2. The Neotropical rainforest biome does not appear to expand toward temperate latitudes during extreme warming events, even when temperatures in temperate regions are within the tropical range. Insolation can be a strong constraint for the latitudinal migration of the TRF biome.
3. The fossil record of Neotropical rainforests indicates that the biome coped with intense warming events (an increase of $\sim 5\text{--}7^\circ\text{C}$ over modern values), in contrast with models predicting a collapse of TRFs.
4. During the Cenozoic, there was significant increase in diversity associated with a significant increase in temperature, at both short ($\sim 200\text{-ka}$) and long ($2\text{--}4\text{-Ma}$) timescales. The increase in temperature could speed up biochemical kinetics and rates of molecular evolution, which, together with stronger biotic interactions, could promote speciation. Temperature seems to be an ultimate driver of rates of speciation.

FUTURE ISSUES

1. The paleobotanical fossil record of South America is excellent across all latitudes. We need far more quantitative data points in several basins from latitudes 5°N to 35°S to track how South American biomes have evolved over time, not only during warming events but also during Neogene cooling events.
2. It is important to explore the response of tropical plant communities to the extreme warming during the mid-Cretaceous. Cretaceous floristic composition is completely different from that of modern TRFs, with gymnosperms and ferns dominating the landscape. Do they respond to warming as Cenozoic angiosperms did? Do they increase in diversity as well?
3. What is the ecophysiological behavior of the Mixed Paleoflora, those floras, without a modern analog, that developed in midlatitudes of South America during global warming events?
4. Many more empirical determinations of MAT are needed from the tropics, especially during the late Oligocene to late Miocene interval, a time of major changes in world climate.

DISCLOSURE STATEMENT

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LITERATURE CITED

- Aber J, Neilson R, McNulty S, Lenihan JM, Bachelet D, Draper RJ. 2001. Forest processes and global environmental change: predicting the effects of individual and multiple stressors. *BioScience* 51:735–51
- Allen PA, Gillooly JF, Savage VM, Brown JH. 2006. Kinetic effects of temperature on rates of genetic divergence and speciation. *Proc. Natl. Acad. Sci. USA* 103:9130–35
- Arakaki M, Christin P-A, Nyffeler R, Lendel A, Eggli U, et al. 2011. Contemporaneous and recent radiations of the world's major succulent plant lineages. *Proc. Natl. Acad. Sci. USA* 108:8379–84
- Archangelsky S. 1973. Palinología del Paleoceno de Chubut. 1. Descripciones sistemáticas. *Ameghiniana* 10:339–99
- Archangelsky S, Romero EJ. 1974. Polen de gimnospermas (coníferas) del Cretácico superior y Paleoceno de Patagonia. *Ameghiniana* 11:217–36
- Archangelsky S, Zamalao MC. 1986. Nuevas descripciones palinológicas de las formaciones Salamanca y Bororó, Paleoceno de Chubut (República Argentina). *Ameghiniana* 23:35–46

- Báez AM, Zamaloa MC, Romero EJ. 1990. Nuevos hallazgos de microfloras y anuros paleógenos en el noroeste de Patagonia: implicancias paleoambientales y paleogeográficas. *Ameghiniana* 27:83–94
- Barracough TG, Savolainen V. 2001. Evolutionary rates and species diversity in flowering plants. *Evolution* 55:677–83
- Bassow SL, McConnaughay KD, Bazzaz FA. 1994. The response of temperate tree seedlings grown in elevated CO₂ to extreme temperature events. *Ecol. Appl.* 4:593–603
- Beerling DJ, Woodward FI. 2001. *Vegetation and the Terrestrial Carbon Cycle: Modelling the First 400 Million Years*. Cambridge, UK: Cambridge Univ. Press. 405 pp.
- Berry J, Björkman O. 1980. Photosynthetic response and adaptation to temperature in higher plants. *Annu. Rev. Plant Physiol.* 31:491–543
- Bloch J, Cadena E, Hasting A, Rincón A, Jaramillo C. 2008. *New vertebrate faunas from the Paleocene sediments of Colombia, Northwestern South America*. Presented at Annu. Meet. Soc. Vertebr. Paleontol., 68th, Clevel.
- Bowen GJ, Zachos JC. 2010. Rapid carbon sequestration at the termination of the Palaeocene–Eocene Thermal Maximum. *Nat. Geosci.* 3:866–69
- Boyce CK, Lee J-E. 2010. An exceptional role for flowering plant physiology in the expansion of tropical rainforests and biodiversity. *Proc. R. Soc. B* 277:3437–43
- Boyden JA, Müller RD, Gurnis M, Torsvik TH, Clark JA, et al. 2011. Next-generation plate-tectonic reconstructions using GPlates. In *Geoinformatics: Cyberinfrastructure for the Solid Earth Sciences*, ed. GR Keller, C Baru, pp. 95–113. Cambridge, UK: Cambridge Univ. Press
- Brodribb TJ, Feild TS. 2010. Leaf hydraulic evolution led a surge in leaf photosynthetic capacity during early angiosperm diversification. *Ecol. Lett.* 13:175–83
- Bromham L, Cardillo M. 2003. Testing the link between the latitudinal gradient in species richness and rates of molecular evolution. *J. Evol. Biol.* 16:200–7
- Burnham RJ, Johnson KR. 2004. South American palaeobotany and the origins of Neotropical rainforests. *Philos. Trans. R. Soc. B* 359:1595–610
- Cadena E, Bloch J, Jaramillo C. 2010. New Podocnemidid turtle (Testudines: Pleurodira) from the middle–upper Paleocene of South America. *J. Vertebr. Paleontol.* 30:367–82
- Cadena E, Bloch J, Jaramillo C. 2012a. New Bothremydid turtle (Testudines, Pleurodira) from the Paleocene of northeastern Colombia. *J. Paleontol.* 86:689–98
- Cadena E, Jaramillo C. 2006. *New Podocnemididae fossil turtles from the late Paleocene Cerrejón Formation, Guajira Peninsula, Colombia*. Presented at Annu. Meet. Soc. Vertebr. Paleontol., 66th, Ottawa, Can.
- Cadena E, Ksepka DT, Jaramillo C, Bloch JI. 2012b. New Pelomedusoid turtles (Testudines, Panpleurodira) from the late Palaeocene Cerrejón Formation of Colombia and implications for phylogeny and body size evolution. *J. Syst. Paleontol.* 10:313–31
- Carvalho M, Herrera F, Jaramillo C, Wing S, Callejas R. 2011. Paleocene Malvaceae from northern South America and their biogeographical implications. *Am. J. Bot.* 98:1337–55
- Cernusak LA, Winter K, Martínez C, Correa E, Aranda J, et al. 2011. Responses of legume versus nonlegume tropical tree seedlings to elevated CO₂ concentration. *Plant Physiol.* 157:372–85
- Chao A, Chazdon RL, Colwell RK, Shen T. 2006. Abundance-based similarity indices and their estimation when there are unseen species in samples. *Biometrics* 62:361–71
- Cheesman AW, Winter K. 2013. Elevated night-time temperatures increase growth in seedlings of two tropical pioneer tree species. *New Phytol.* 197:1185–92
- Comita LS, Muller-Landau HC, Aguilar S, Hubbell SP. 2010. Asymmetric density dependence shapes species abundances in a tropical tree community. *Science* 329:330–32
- Connell JH. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In *Dynamics of Populations*, ed. PJ den Boer, GR Gradwell, pp. 298–312. Wageningen, Neth.: Cent. Agric. Publ. Doc.
- Cox PM, Betts RA, Collins M, Harris PP, Huntingford C, Jones CD. 2004. Amazonian forest dieback under climate-carbon cycle projections for the 21st century. *Theor. Appl. Climatol.* 78:137–56
- Crane PR, Lidgard S. 1989. Angiosperm diversification and paleolatitudinal gradients in Cretaceous floristic diversity. *Science* 246:675–78
- Davies TJ, Savolainen V, Chase MW, Moat J, Barracough TG. 2004. Environmental energy and evolutionary rates in flowering plants. *Proc. R. Soc. B* 271:2195–200

- D'Hondt S, Arthur MA. 1996. Late Cretaceous oceans and the cool tropic paradox. *Science* 271:1838–41
- Diefendorf AF, Mueller KE, Wing SL, Koch PL, Freeman KH. 2010. Global patterns in leaf ^{13}C discrimination and implications for studies of past and future climate. *Proc. Natl. Acad. Sci. USA* 107:5738–43
- Dobzhansky T. 1950. Evolution in the tropics. *Am. Sci.* 38:209–21
- Doria G, Jaramillo C, Herrera F. 2008. Menispermaceae from the Cerrejón Formation, middle to late Paleocene, Colombia. *Am. J. Bot.* 95:954–73
- Dorman JL, Sellers PJ. 1989. A global climatology of albedo, roughness length and stomatal resistance for atmospheric general circulation models as represented by the Simple Biosphere Model (SiB). *J. Appl. Meteorol.* 28:833–55
- Edwards EJ, Osborne CP, Strömberg CAE, Smith SA, C₄ Grasses Consortium. 2010. The origins of C₄ grasslands: integrating evolutionary and ecosystem science. *Science* 328:587–91
- Enquist BJ, Haskell JP, Tiffney BH. 2002. General patterns of taxonomic and biomass partitioning in extant and fossil plant communities. *Nature* 419:610–13
- Evans KL, Warren PH, Gaston KJ. 2005. Species–energy relationships at the macroecological scale: a review of the mechanisms. *Biol. Rev.* 80:1–25
- Feild TS, Brodribb TJ, Iglesias A, Chatelet DS, Baresh A, et al. 2011. Fossil evidence for Cretaceous escalation in angiosperm leaf vein evolution. *Proc. Natl. Acad. Sci. USA* 108:8363–66
- Fine PVA, Ree RH. 2006. Evidence for a time-integrated species-area effect on the latitudinal gradient in tree diversity. *Am. Nat.* 168:796–804
- Fine PVA, Ree RH, Burnham RJ. 2008. Disparity in tree species richness between tropical, temperate and boreal biomes: the geographic area and age hypothesis. In *Tropical Forest Community Ecology*, ed. WP Carson, SA Schnitzer, pp. 31–45. London: Blackwell
- Frakes LA, Francis JE, Syktus JI. 1992. *Climate Modes of the Phanerozoic*. Cambridge, UK: Cambridge Univ. Press. 288 pp.
- Francis AP, Currie DJ. 2003. A globally consistent richness–climate relationship for angiosperms. *Am. Nat.* 161:523–36
- Friedrich O, Norris RD, Erbacher J. 2012. Evolution of middle to Late Cretaceous oceans—a 55 m.y. record of Earth's temperature and carbon cycle. *Geology* 40:107–10
- Gentry AH. 1988. Changes in plant community diversity and floristic composition on environmental and geographical gradients. *Ann. Mo. Bot. Garden* 75:1–34
- Gingerich PD. 2006. Environment and evolution through the Paleocene-Eocene Thermal Maximum. *Trends Ecol. Evol.* 21:246–53
- Gomez N, Jaramillo C, Herrera F, Wing SL, Callejas R. 2009. Palms (Arecaceae) from a Paleocene rainforest of northern Colombia. *Am. J. Bot.* 96:1300–12
- Graham A. 2010. *Late Cretaceous and Cenozoic History of Latin American Vegetation and Terrestrial Environments*. St Louis: Mo. Bot. Garden Press
- Harris PP, Huntingford C, Cox PM. 2008. Amazon Basin climate under global warming: the role of the sea surface temperature. *Philos. Trans. R. Soc. B* 363:1753–59
- Hasting A, Bloch J, Cadena E, Jaramillo C. 2010. A new small short-snouted dyrosaurid (Crocodylomorpha, Mesoeucrocodylia) from the Paleocene of northeastern Colombia. *J. Vertebr. Paleontol.* 30:139–62
- Hasting A, Bloch J, Jaramillo C. 2011. A new longirostrine dyrosaurid (Crocodylomorpha, Mesoeucrocodylia) from the Paleocene of north-eastern Colombia: biogeographic and behavioural implications for New-World Dyrosauridae. *Palaentology* 54:1095–116
- Hastings D, Russell A, Emerson S. 1998. Foraminiferal magnesium in *Globeriginoides sacculifer* as a paleotemperature proxy. *Paleoceanography* 13:161–69
- Head J, Bloch J, Hasting A, Bourque J, Cadena E, et al. 2009a. Giant boid snake from the Palaeocene neotropics reveals hotter past equatorial temperatures. *Nature* 457:715–17
- Head J, Bloch J, Hasting A, Bourque J, Cadena E, et al. 2009b. Reply: Giant boid snake from the Palaeocene neotropics reveals hotter past equatorial temperatures. *Nature* 460:E4–5
- Herrera F, Jaramillo C, Dilcher D, Wing SL, Gomez C. 2008. Fossil Araceae from a Paleocene Neotropical rainforest in Colombia. *Am. J. Bot.* 95:1569–83
- Herrera F, Manchester SR, Hoot SB, Wefferling K, Carvalho M, Jaramillo C. 2011. Phylogeographic implications of fossil endocarps of Menispermaceae from the Paleocene of Colombia. *Am. J. Bot.* 98:1–14

- Higgins SI, Scheiter S. 2012. Atmospheric CO₂ forces abrupt vegetation shifts locally, but not globally. *Nature* 488:209–12
- Hinojosa F, Villagran C. 2005. Did South American Mixed Paleofloras evolve under thermal equability or in the absence of an effective Andean barrier during the Cenozoic? *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 217:1–23
- Huber M. 2008. A hotter greenhouse? *Science* 321:353–54
- Huber M. 2009. Snakes tell a torrid tale. *Nature* 457:669–71
- Huber M, Caballero R. 2011. The early Eocene equable climate problem revisited. *Clim. Past Discuss.* 7:603–33
- Huber M, Sloan LC. 1999. Warm climate transitions: a general circulation modeling study of the Late Paleocene Thermal Maximum (~56 Ma). *J. Geophys. Res.* 104:16633–55
- Huber M, Sloan LC. 2000. Climatic responses to tropical sea surface temperature changes on a ‘greenhouse’ Earth. *Paleoceanography* 15:443–50
- Huber M, Sloan LC, Shellito C. 2003. Early Paleogene oceans and climate: a fully coupled modeling approach using the NCAR CCSM. In *Causes and Consequences of Globally Warm Climates in the Early Paleogene*, ed. SL Wing, PD Gingerich, B Schmitz, E Thomas, pp. 25–47. Boulder, CO: Geol. Soc. Am.
- Iglesias A, Artabe AE, Morel EM. 2011. The evolution of Patagonian climate and vegetation from the Mesozoic to the present. *Biol. J. Linn. Soc.* 103:409–22
- Iglesias A, Wilf P, Johnson KR, Zamuner AB, Cúneo NR, et al. 2007. A Paleocene lowland macroflora from Patagonia reveals significantly greater richness than North American analogs. *Geology* 35:947–50
- Jablonski D. 1993. The tropics as a source of evolutionary novelty through geological time. *Nature* 364:142–44
- Janzen DH. 1970. Herbivores and the number of tree species in tropical forests. *Am. Nat.* 104:501–28
- Jaramillo C, Ochoa D, Contreras L, Pagani M, Carvajal-Ortiz H, et al. 2010. Effects of rapid global warming at the Paleocene-Eocene boundary on Neotropical vegetation. *Science* 330:957–61
- Jaramillo C, Rueda M, Mora G. 2006. Cenozoic plant diversity in the Neotropics. *Science* 311:1893–96
- Jaramillo CA. 2002. Response of tropical vegetation to Paleogene warming. *Paleobiology* 28:222–43
- Jaramillo CA, Dilcher DL. 2000. Microfloral diversity patterns of the late Paleocene-Eocene interval in Colombia, northern South America. *Geology* 28:815–18
- Jaramillo CA, Dilcher DL. 2001. Middle Paleogene palynology of central Colombia, South America: a study of pollen and spores from tropical latitudes. *Palaeontogr. Abt. B* 258:87–213
- Johnson DJ, Beaulieu WT, Bever JD, Clay K. 2012. Conspecific negative density dependence and forest diversity. *Science* 336:904–7
- Josse C, Navarro G, Comer P, Evans R, Faber-Langendoen D, et al. 2003. *Ecological Systems of Latin America and the Caribbean: A Working Classification of Terrestrial Systems*. Arlington, VA: NatureServe
- Kim J, Schouten S, Hopmans EC, Donner B, Sinninghe Damsté JS. 2008. Global core-top calibration of the TEX₈₆ paleothermometer in the ocean. *Geochim. Cosmochim. Acta* 72:1154–73
- Kim J-H, van der Meer J, Schouten S, Helmke P, Willmott V, et al. 2010. New indices and calibrations derived from the distribution of crenarchaeal isoprenoid tetraether lipids: implications for past sea surface temperature reconstructions. *Geochim. Cosmochim. Acta* 74:4639–54
- Krause GH, Winter K, Krause B, Jahns P, Garcia M, et al. 2010. High-temperature tolerance of a tropical tree, *Ficus insipida*: methodological reassessment and climate change considerations. *Funct. Plant Biol.* 37:890–900
- Leigh EG, Davider P, Dick C, Puyravaud J, Terborgh J, et al. 2004. Why do some tropical forests have so many species of trees? *Biotropica* 36:447–73
- Lerdau MT, Throop HL. 1999. Isoprene emissions and photosynthesis in a tropical forest canopy: implications for model development. *Ecol. Appl.* 109:1109–17
- Lewis SL, Malhi Y, Phillips OL. 2004. Fingerprinting the impacts of global change on tropical forests. *Philos. Trans. R. Soc. B* 359:437–62
- Liu Z, Pagani M, Zinniker D, DeConto R, Huber BT, et al. 2009. Global cooling during the Eocene-Oligocene climate transition. *Science* 323:1187–90
- Lloyd J, Farquhar GD. 2008. Effects of rising temperatures and [CO₂] on the physiology of tropical forest trees. *Philos. Trans. R. Soc. B* 363:1811–17
- MacArthur RH. 1961. Population effects of natural selection. *Am. Nat.* 95:195–99

- Magurran AE. 2004. *Measuring Biological Diversity*. Malden, MA: Blackwell. 256 pp.
- Majure LC, Punete R, Griffith MP, Judd WS, Soltis PS, Soltis DE. 2012. Phylogeny of *Opuntia* s.s. (Cactaceae): clade delination, geographic origins, and reticulate evolution. *Am. J. Bot.* 99:847–64
- Mangan SA, Schnitzer SA, Herre EA, Mack KML, Valencia MC, et al. 2010. Negative plant-soil feedback predicts tree-species relative abundance in a tropical forest. *Nature* 466:752–55
- Melendi DL, Scafati LH, Volkheimer W. 2003. Palynostratigraphy of the Paleogene Huitrera Formation in N-W Patagonia, Argentina. *N. Jahrb. Geol. Paläont. Abb.* 228:205–73
- Menéndez C, Caccavari de Filice M. 1975. Las especies de *Nothofagidites* (polen fósil de *Nothofagus*) de sedimentos Terciarios y Cretácicos de Estancia La Sara, norte de Tierra del Fuego, Argentina. *Ameghiniana* 12:165–83
- Mittelbach GG, Schemske DW, Cornell HV, Allen AP, Brown JM, et al. 2007. Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecol. Lett.* 10:315–31
- Moles AT, Wallis IR, Foley WJ, Warton DI, Stegen JC, et al. 2011. Putting plant resistance traits on the map: a test of the idea that plants are better defended at lower latitudes. *New Phytol.* 191:777–88
- Moles AT, Westoby M. 2003. Latitude, seed predation and seed mass. *J. Biogeogr.* 30:105–28
- Morley RJ. 2000. *Origin and Evolution of Tropical Rain Forests*. New York: Wiley. 362 pp.
- Niu S, Wu M, Han Y, Xia J, Li L, Wan S. 2008. Water-mediated responses of ecosystem carbon fluxes to climatic change in a temperate steppe. *New Phytol.* 177:209–19
- Ochoa D, Hoorn C, Jaramillo C, Bayona G, De la Parra F, Parra M. 2012. The final phase of tropical lowland conditions in the axial zone of the Eastern Cordillera of Colombia: evidence from three palynological records. *J. S. Am. Earth Sci.* 39:157–69
- Oksanen J, Blanchet FG, Kindt R, Legendre RG, O'Hara B, et al. 2010. Community ecology package. In *R for Statistical Computing, R package version 1.17-0*. Vienna: R Found. Stat. Comput. <http://CRAN.R-project.org/package=vegan>
- Osborne PL. 2000. *Tropical Ecosystems and Ecological Concepts*. Cambridge, UK: Cambridge Univ. Press. 464 pp.
- Pardo-Trujillo A, Jaramillo CA, Oboh-Ikuenobe F. 2003. Paleogene palynostratigraphy of the eastern Middle Magdalena Valley, Colombia. *Palynology* 27:155–78
- Pearson PN, Ditchfield PW, Singano J, Harcourt-Brown KG, Nicholas CJ, et al. 2001. Warm tropical sea surface temperatures in the Late Cretaceous and Eocene epochs. *Nature* 413:481–87
- Pennington RT, Lewis GP, Ratter JA. 2006. An overview of the plant diversity, biogeography and conservation of Neotropical savannas and seasonally dry forests. In *Neotropical Savannas and Seasonally Dry Forests: Plant Diversity, Biogeography, and Conservation*, ed. RT Pennington, GP Lewis, JA Ratter, pp. 1–30. Boca Raton, FL: Taylor & Francis
- Peppe DJ, Royer DL, Cariglino B, Oliver SY, Newman S, et al. 2011. Sensitivity of leaf size and shape to climate: global patterns and paleoclimatic applications. *New Phytol.* 190:724–39
- Phillips O, James M, Gentry A. 2002. *Global Patterns of Plant Diversity: Alwyn H. Gentry's Forest Transect Data Set*. St. Louis: Missouri Bot. Garden Press. 319 pp.
- Pucéat E, Lécuyer C, Donnadiou Y, Naveau P, Cappetta H, et al. 2007. Fish tooth $\delta^{18}\text{O}$ revising Late Cretaceous meridional upper ocean water temperature gradients. *Geology* 35:107–10
- R Dev. Core Team. 2012. *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Found. Stat. Comput.
- Ramirez SR, Gravendeel B, Singer RB, Marshall CR, Pierce NE. 2007. Dating the origin of the Orchidaceae from a fossil orchid with its pollinator. *Nature* 448:1042–45
- Ricklefs RE. 2004. A comprehensive framework for global patterns in biodiversity. *Ecol. Lett.* 7:1–15
- Ricklefs RE, Renner SS. 2012. Global correlations in tropical tree species richness and abundance reject neutrality. *Science* 335:464–67
- Rodríguez-Forero G, Oboh-Ikuenobe FE, Jaramillo-Munoz C, Rueda-Serrano MJ, Cadena-Rueda E. 2012. Palynology of the Eocene Esmeraldas Formation, Middle Magdalena Valley Basin, Colombia. *Palynology* 36:S96–111
- Rohde K. 1992. Latitudinal gradients in species diversity—the search for the primary cause. *Oikos* 65:514–27
- Romero EJ. 1977. *Polen de Gimnospermas y Fagáceas de la Formación Río Turbio (Eoceno), Santa Cruz, Argentina*. Buenos Aires: Fundación para la Educación, la Ciencia y la Cultura. 219 pp.

- Romero EJ. 1978. Paleoecología y paleofitogeografía de las taofloras del Cenofítico de Argentina y áreas vecinas. *Ameghiniana* 15:209–27
- Romero EJ. 1986. Paleogene phytogeography and climatology of South America. *Ann. Mo. Bot. Garden* 73:449–61
- Romero EJ. 1993. South American Paleofloras. In *Biological Relationships between Africa and South America*, ed. P Goldblatt, pp. 62–85. New Haven, CT: Yale Univ. Press
- Romero EJ, Castro M. 1986. Material fúngico y granos de polen de angiospermas de la Formación Río Turbio (Eoceno), provincia de Santa Cruz, República Argentina. *Ameghiniana* 23:101–18
- Romero EJ, Zamalao MC. 1985. Polen de angiospermas de la Formación Río Turbio (Eoceno), Provincia de Santa Cruz, Argentina. *Ameghiniana* 22:43–51
- Rosenzweig ML. 1995. *Species Diversity in Space and Time*. Cambridge, UK: Cambridge Univ. Press. 433 pp.
- Roy K, Jablonski D, Valentine JW. 2000. Dissecting latitudinal diversity gradients: functional groups and clades of marine bivalves. *Proc. R. Soc. B* 267:293–99
- Roy K, Jablonski D, Valentine JW, Rosenberg G. 1998. Marine latitudinal diversity gradients: test of causal hypothesis. *Proc. Natl. Acad. Sci. USA* 95:3699–702
- Royer DL. 2006. CO₂-forced climate thresholds during the Phanerozoic. *Geochim. Cosmochim. Acta* 70:5665–75
- Royer DL. 2010. Fossil soils constrain ancient climate sensitivity. *Proc. Natl. Acad. Sci. USA* 107:517–18
- Royer DL, Sack L, Wilf P, Lusk CH, Jordan GJ, et al. 2007. Fossil leaf economics quantified: calibration, Eocene case study, and implications. *Paleobiology* 33:574–89
- Schemske D. 2009. Biotic interactions and speciation in the tropics. In *Speciation and Patterns of Diversity*, ed. R Butlin, J Bridle, D Schluter, pp. 1–21. Cambridge, UK: Cambridge Univ. Press
- Schouten S, Huguët C, Hophmans EC, Kienhuis MVM, Sinninghe Damsté JS. 2007. Improved analytical methodology of the TEX₈₆ paleothermometry by high-performance liquid chromatography/atmospheric pressure chemical ionization-mass spectrometry. *Anal. Chem.* 79:2940–44
- Schuettpelz E, Pryer KM. 2009. Evidence for a Cenozoic radiation of ferns in an angiosperm-dominated canopy. *Proc. Natl. Acad. Sci. USA* 106:11200–5
- Schultz T, Brady S. 2008. Major evolutionary transitions in ant agriculture. *Proc. Natl. Acad. Sci. USA* 105:5435–40
- Scotese CR. 2003. *PALEOMAP Project*. Arlington, Texas. <http://www.scotese.com>
- Sewall JO, Sloan LC, Huber M, Wing S. 2000. Climate sensitivity to changes in land surface characteristics. *Glob. Planet. Change* 26:445–65
- Sexton PF, Wilson PA, Pearson PN. 2006. Microstructural and geochemical perspectives on planktic foraminiferal preservation: ‘glassy’ versus ‘frosty’. *Geochem. Geophys. Geosyst.* 7:Q12P19
- Shellito CJ, Sloan LC, Huber M. 2003. Climate model sensitivity to atmospheric CO₂ levels in the early-middle Paleogene. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 193:113–23
- Simon MF, Grether R, de Queiroz L, Skema C, Pennington ET, Hughes CE. 2009. Recent assembly of the Cerrado, a Neotropical plant diversity hotspot, by in situ evolution of adaptations to fire. *Proc. Natl. Acad. Sci. USA* 106:20359–64
- Sloan LC, Barron EJ. 1992. A comparison of Eocene climate model results to quantified paleoclimatic interpretations. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 93:183–202
- Sloan LC, Morrill C. 1998. Orbital forcing and Eocene continental temperatures. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 144:21–35
- Sloan LC, Rea DK. 1995. Atmospheric carbon dioxide and early Eocene climate: a general circulation modeling sensitive study. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 119:275–92
- Sloan LC, Thomas E. 1998. Global climate of the late Paleocene epoch: modeling the circumstances associated with a climatic ‘event.’ In *Late Paleocene–Early Eocene Climatic and Biotic Events in the Marine and Terrestrial Records*, ed. MP Aubry, SG Lucas, WA Berggren, pp. 138–57. New York: Columbia Univ. Press
- Sloan LC, Walker JC, Moore TC. 1995. Possible role of oceanic heat transport in early Eocene climate. *Paleoceanography* 10:347–56
- Stebbins GL. 1974. *Flowering Plants: Evolution Above the Species Level*. Cambridge, MA: Harvard Univ. Press. 399 pp.

- Stoskopf N. 1981. *Understanding Crop Production: Upper Saddle River*. Reston, VA: Reston. 433 pp.
- Stull GW, Herrera F, Manchester S, Jaramillo C, Tiffney BH. 2012. Fruits of an 'Old World' tribe (Phytocreneae; Icacinaceae) from the Paleogene of North and South America. *Syst. Bot.* 37:784–94
- Terborgh J. 1973. On the notion of favorableness in plant ecology. *Am. Nat.* 107:481–501
- Tewksbury JJ, Huey RB, Deutsch CA. 2008. Putting the heat on tropical animals. *Science* 320:1296–97
- Thomas WW. 1999. Conservation and monographic research on the flora of tropical America. *Biodivers. Conserv.* 8:1007–15
- Tripathi A, Delaney ML, Zachos JC, Anderson LD, Kelly DC, Elderfield H. 2003. Tropical sea-surface temperature reconstruction for the early Paleogene using Mg/Ca ratios of planktonic foraminifera. *Paleoceanography* 18:1101–14
- Utescher T, Mosbrugger V. 2007. Eocene vegetation patterns reconstructed from plant diversity—a global perspective. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 247:243–71
- Vermeij GJ. 2003. Temperature, tectonics, and evolution. In *Evolution on Planet Earth: The Impact of the Physical Environment*, ed. LJ Rothschild, A Lister, pp. 209–32. Amsterdam: Academic
- Vermeij GJ. 2005. From phenomenology to first principles: toward a theory of diversity. *Proc. Calif. Acad. Sci.* 56(Suppl. I, No. 2):12–23
- Volkheimer W, Novara MG, Narváez PL, Marquillas RA. 2006. Palynology and paleoenvironmental significance of the Tunal Formation (Danian) at its type locality, El Chorro Creek (Salta, Argentina). *Ameghiniana* 43:567–84
- Volkheimer W, Scafati L, Melendi DL. 2007. Palynology of a Danian warm climatic wetland in central northern Patagonia, Argentina. *Rev. Española Micropaleontol.* 39:117–34
- Wilf P, Cúneo NR, Johnson KR, Hicks JF, Wing SL, Obradovich JD. 2003. High plant diversity in Eocene South America: evidence from Patagonia. *Science* 300:122–25
- Wilf P, Johnson KR, Cúneo NR, Smith ME, Singer BS, Gandolfo M. 2005. Eocene plant diversity at Laguna del Hunco and Rio Pichileufu, Patagonia, Argentina. *Am. Nat.* 165:634–50
- Willig MR, Kaufman DM, Stevens RD. 2003. Latitudinal gradients of biodiversity: patterns, process, scale, and synthesis. *Annu. Rev. Ecol. Evol. Syst.* 34:273–309
- Willis KJ, McElwain JC. 2002. *The Evolution of Plants*. New York: Oxford Univ. Press
- Wing SL, Herrera F, Jaramillo C, Gomez C, Wilf P, Labandeira CC. 2009. Late Paleocene fossils from the Cerrejón Formation, Colombia, are the earliest record of Neotropical rainforest. *Proc. Natl. Acad. Sci. USA* 106:18627–32
- Wolfe JA. 1979. Temperature parameters of humid to mesic forests of eastern Asia and relation to forests of other regions in the Northern Hemisphere and Australasia. *U.S. Geol. Surv. Prof. Pap.* 1106:1–37
- Wolfe JA. 1985. Distribution of major vegetational types during the Tertiary. In *The Carbon Cycle and Atmospheric CO₂: Natural Variations Archean to Present*, ed. ET Sundquist, WS Broecker, *Geophys. Monogr.* 32:357–75. Washington, DC: AGU
- Wright DH. 1983. Species-energy theory: an extension of species-area theory. *Oikos* 41:496–506
- Wright DH, Currie DJ, Maurer BA. 1993. Energy supply and patterns of species richness on local and regional scales. In *Species Diversity in Ecological Communities: Historical and Geographical Perspectives*, ed. RE Ricklefs, D Schluter, pp. 66–74. Chicago: Univ. Chicago Press
- Wright S, Keeling J, Gillman L. 2006. The road from Santa Rosalia: a faster tempo of evolution in tropical climates. *Proc. Natl. Acad. Sci. USA* 103:7718–22
- Zachos J, Pagani M, Sloan L, Thomas E, Billups K. 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science* 292:686–93
- Zachos JC, Arthur MA, Bralower TJ, Spero HJ. 2002. Tropical temperatures in greenhouse episodes. *Nature* 419:897–98
- Zachos JC, Wara MW, Bohaty S, Delaney ML, Petrizzo MR, et al. 2003. A transient rise in tropical sea surface temperature during the Paleocene-Eocene Thermal Maximum. *Science* 302:1551–54
- Ziegler AM, Eshel G, Rees PM, Rothfus TA, Rowley DB, Sunderlin D. 2003. Tracing the tropics across land and sea: Permian to present. *Lethaia* 36:227–54



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