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Key Points:

- Rifting of West Gondwana initiated the Atlantic Intertropical Convergence Zone and altered the South American and African monsoons
- Simulations of Cenomanian, early Eocene, and middle Miocene indicate paleogeography instead of CO₂ control monsoon distribution
- Through time, changes in South American and African monsoon circulation influenced the evolution of the Amazon and African rainforests

Supporting Information:

Supporting Information may be found in the online version of this article.

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Evolution of the Atlantic Intertropical Convergence Zone, and the South American and African Monsoons Over the Past 95-Myr and Their Impact on the Tropical Rainforests

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Abstract The widening of the South Atlantic Basin led to the reorganization of regional atmospheric and oceanic circulations. However, the response of the Atlantic Intertropical Convergence Zone (ITCZ), and South American and African monsoons across paleoclimate states, especially under constant paleogeographic and climatic changes, has not been well understood. Here we report on paleoclimate simulations of the Cenomanian (~95 Ma), early Eocene (~55 Ma), and middle Miocene (~14 Ma) using the Community Earth System Model version 1.2 to understand how the migration of the South American and African continents to their modern-day positions, uplift of the Andes and East African Rift Zone, and the decline of atmospheric CO₂ changed the Atlantic ITCZ, and the South American and African monsoons and rainforests. Our work demonstrates that the South Atlantic widening developed the Atlantic ITCZ. The South Atlantic widening and Andean orogeny led to a stronger South American monsoon. We find the orogeny of the East African Rift Zone is the primary mechanism that strengthened the East African monsoon, whereas the West African monsoon became weaker through time as West Africa migrated toward the subtropics and CO₂ levels fell below 500 ppm. We utilize the Köppen-Geiger Climate Classification as an indicator for maximum rainforest extent. We find that during the Cenomanian and early Eocene, a Pan-African rainforest existed, while the Amazon rainforest was restricted toward the northwestern corner of South America. During the middle Miocene, the Pan-African rainforest was reduced to near its modern-day size, while the Amazon rainforest expanded eastward.

Plain Language Summary The rifting of the West Gondwana supercontinent from the middle Cretaceous led to the opening of the South Atlantic Basin and the reorganization of regional atmospheric and oceanic circulations. However, the evolution of the South American and African continents under constant paleogeographic and climatic changes has not been well understood. Here we report on paleoclimate simulations since the middle Cretaceous using the Community Earth System Model version 1.2 to understand how the widening of the South Atlantic Basin, uplift of the Andes and East African Rift Zone, and CO₂ decline through time influenced the Atlantic Intertropical Convergence Zone (ITCZ), and the South American and African monsoons and rainforests. Our results suggest that both changes in geography and topography have a first-order control on the rainfall distribution of the Atlantic ITCZ, South American, and African monsoon. Increased atmospheric CO₂ in the past enhanced tropical precipitation, but it does not determine where it occurs. Our work shows that when the South Atlantic Basin was narrowed, the eastern Amazon rainforest did not exist, while a Pan-African rainforest expanded toward the subtropics. As the South Atlantic Basin widened, the eastern Amazon rainforest formed, while the Pan-African rainforest shrunk to its modern-day size.

1. Introduction

The seasonal, cross-hemisphere migration of the Atlantic Intertropical Convergence Zone (ITCZ) and its transition into distinct tropical monsoon systems, the South American and the African monsoons, delivers substantial precipitation into the South American and African continents. These atmospheric circulations drive continental hydroclimate and consequently regulate the expansion and contraction of the regional tropical rainforest systems. The ITCZ and monsoons are strongly influenced by the position of the surrounding landmasses (Gill, 1980; Privé & Plumb, 2007b), which differed substantially in the past (Pletsch et al., 2001; Seton et al., 2012). For example, based on paleoclimate simulations of the late Paleozoic and early Mesozoic (~250 Ma), when the South American and African continents was the West Gondwana mega-continent, a single “mega-monsoon” system

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determined the hydrological cycle (Kutzbach & Gallimore, 1989; Peyser & Poulsen, 2008). Understanding the transition from the Gondwana “mega-monsoon” circulation toward the modern Atlantic ITCZ and monsoon systems can shed light on the evolution of the South American and African hydroclimate systems. Additionally, as the South American and African continents migrated toward their modern-day positions, regional topography and climate were also in flux, further adding complexity to the system. Our work aims to disentangle the role of continental drift, orography, and CO₂, as the modern-day Atlantic ITCZ and South American and African monsoons evolved through time. In doing so, we can then discuss how the evolution of the regional hydroclimate system shaped Amazonian and African rainforests.

The ITCZ is part of the tropical ascending branch of the Northern and Southern Hemisphere Hadley Cells circulations coinciding with regions of maximum sea surface temperatures (SSTs). The strong low-level (~850 mb) convergence via tropical easterly winds feeds moisture to tropical convective systems and produces a substantial amount of rainfall (Geen et al., 2020). Today, the Atlantic ITCZ seasonally migrates between 10°N (boreal summer) and 10°S (austral summer) and brings rain to the eastern coast of South America and the coast of West Africa. Meanwhile, continental monsoon systems are seasonal off-equatorial displaced rising branches of the Hadley cell, associated with seasonal precipitation and wind reversals (Gadgil, 2018). The South American monsoon extends down to 30°S during the austral summer months (December–February; DJF). Precipitation from the South American monsoon enables the modern Amazon rainforest to span the entire northern half of South America and terminates at ~10°S (Peel et al., 2007). The African monsoon is typically divided into several distinct monsoon regimes, the West African monsoon, which extends northward to 15°N during boreal summer months (June–August; JJA), and the East African monsoon that reaches southward to 15°S during austral summer months (Battisti et al., 2018; Geen et al., 2020) and the Central African monsoon as a transitional circulation between the East and West African monsoons (Farnsworth et al., 2011). The African monsoons enable the African rainforest to extend from 5°N to 5°S (Peel et al., 2007). However, through time, changes in South American and African paleogeography, the position of landmasses, and topographies most likely modified the surface and upper-level thermodynamic structure of the atmosphere and Atlantic Ocean circulation, which could have altered the Atlantic ITCZ and the South American and African monsoons.

The rifting of the Gondwana mega-continent initiated paleogeographic changes leading to the present-day configuration (Ziegler et al., 2003). The cleaving of South America and Africa began in the early Jurassic (~200 Ma) and lasted through the early Cretaceous (~145 Ma) (Moulin et al., 2010; Seton et al., 2012). A shallow marine corridor first appeared around the middle Cretaceous (~100 Ma) and formed a narrow South Atlantic Basin, which widened through the Cenozoic (Pletsch et al., 2001). Additionally, the African plate experienced counterclockwise rotation and northwestward movement, while the South American plate moved northeastward (Seton et al., 2012). As the South American and the African continents moved to their modern-day positions, orogens formed that likely further shaped the hydroclimate on the continents. The South American Andes (Boschman, 2021; Garziona et al., 2017; Lossada et al., 2017) and East African Rift System (Jess et al., 2020; Roberts et al., 2012; Wichura et al., 2015) are thought to have reached modern elevations between the early Eocene (~33 Ma) and late Miocene (~7 Ma). Proxy (Garziona et al., 2017; Hoorn et al., 2010) and modeling (Carrapa et al., 2019; Poulsen et al., 2010) evidence suggest that the South American monsoon was strengthened during the Neogene (~20 Ma), coinciding with the uplift of the Andes. Similar evidence (Jung et al., 2016; Linder, 2017; Sepulchre et al., 2006) suggests that the uplift of the East Africa Rift System strengthened the East African monsoon system (Ogwang et al., 2014).

Over the past 95-Myr, in addition to paleogeographic changes, global atmospheric CO₂ levels fluctuated from more than 1,000 ppm during the late Cretaceous and the Paleocene-Eocene boundary (95–55 Ma) (Foster et al., 2017) to well below 400 ppm during the late Miocene (~10 Ma) (Beerling & Royer, 2011). Fluctuation in CO₂ levels is thought to drive the global climatic variability (Foster et al., 2017; Tierney et al., 2020), influencing surface temperatures and the hydrological cycle (Anagnostou et al., 2016; Gaskell et al., 2022). Warmer conditions increase the amount of available atmospheric water vapor relative to the amount precipitated back to the surface (Held & Soden, 2006), suggesting wet regions could have experienced higher precipitation rates while already arid regions could have experienced higher evaporation rates, particularly over the subtropical regions (Scheff et al., 2017). Additionally, a reduced meridional temperature gradient is hypothesized to weaken the Hadley cell overturning circulation (Frierson et al., 2007; Held & Soden, 2006). Such weaker surface wind convergence toward the tropics is hypothesized to produce more in situ precipitation in the subtropics (Burls &

Fedorov, 2017). This previous work suggests that higher CO₂ levels in the past could have led to more subtropical precipitation and perhaps an expansion of tropical rainforest biomes.

The Gondwana breakup changed the strength and locality of the Atlantic ITCZ and South American and African monsoon systems and likely impacted the regional ecosystem. For example, previous paleoclimate simulations of the South American and African monsoon of the late Cretaceous (Bush & Philander, 1997; Ohba & Ueda, 2010), early Eocene (Huber & Goldner, 2012), middle Miocene (Herold et al., 2011), and modern-day (Liu et al., 2019) show a weak Atlantic ITCZ when the South Atlantic Basin was narrow, but overall persistent South American and African monsoons. In support, proxy evidence (Ziegler et al., 2003) suggests the environment over northwest South America and East Africa was dominated by evergreen forests (Morley, 2011). In contrast, pronounced seasonality in rainfall over equatorial Africa suggests the existence of a swamp-like versus tropical rainforest environments. Plant fossil records from the Colombia and Venezuela region indicate that the Amazon rainforest was already established in the northwestern part of South America by the Maastrichtian period (~70 Ma), with species richness peaking during the middle Eocene (~40 Ma) and attaining greater plant diversity than the modern-day Amazon rainforest (Jaramillo et al., 2010). Such an increase in plant diversity has been linked to increased global temperature during the early Cenozoic, when CO₂ levels were well above 1,000 ppm (Beerling & Royer, 2011; Morley, 2011). Meanwhile, a “Pan-African” rainforest is thought to have spanned the width of the African continent and well into the subtropics, with its peak also occurring during the warm house climate of the Cenomanian and the Paleocene-Eocene period (Couvreur et al., 2021). In support, records of angiosperm pollen show an increase in plant species diversity in both South America and Africa during the early Eocene (~55 Ma) (Linder, 2014, 2017).

As CO₂ declined in the middle-to-late Eocene (~38 Ma), records suggest species richness decreased in South America and Africa. However, the South American rainforest system experienced a rebound in species richness during the Neogene, while the African rainforests continued declining (Morley, 2011). Sedimentary records from the Amazon river network suggest that a “Pan-Amazonian” rainforest—spanning across the entirety of northern South America and extending well into the subtropics (30°S)—existed in the late Miocene (~7 Ma) during times when CO₂ levels were much lower, and the climate system was much cooler than the early Cenozoic (Hoorn et al., 2010; Lundberg et al., 1998). The east and southward expansion of the Amazon rainforest with the simultaneous decline of the African rainforest implies that the decrease in global atmospheric CO₂ and associated climatic changes cannot fully explain the regional vegetation changes between the two continents. While much of the literature highlights the role of Andean orography as the dominant mechanism that strengthens the South American monsoon during the Neogene (Garzzone et al., 2017), the role of widening of the South Atlantic Basin (Liu et al., 2019; Ziegler et al., 2003) has been suggested as an additional mechanism that can enhance the South American monsoon.

To understand the role of continental drift, orography, and CO₂ on the hydroclimate system of South America and Africa, we present a systematic analysis of the evolution of the Atlantic ITCZ, South American, and African monsoon circulations over the last 95-Myr. Here, we use time-specific paleogeographic reconstructions of the late Cretaceous (Cenomanian, ~95 Ma), early Eocene (~55 Ma), middle Miocene (~15 Ma), and the preindustrial (PI). We then discuss how changes in paleogeography and CO₂ impacted the South American and African rainforests.

2. Method

2.1. Model

We use the National Center for Atmospheric Research general circulation model (GCM), Community Earth System Model version 1.2 (CESM1.2) (Meehl et al., 2013), a fully coupled global climate model that is equipped with atmosphere, land, river, ocean, and sea-ice components. Specifically, CESM1.2 comprises the Community Atmospheric Model version 5 (CAM5) (Neale et al., 2010), Community Land Model version 4.5 (Oleson et al., 2013), Sea Ice model (Hunke, 2010), Parallel Ocean Program version 2 (Danabasoglu et al., 2012) and a river transport model (Oleson et al., 2013). The simulations were carried out with the finite volume dynamical core version of the atmosphere model with a grid spacing of 1.9° × 2.5° equal to ~200 km over the equator. Ocean and sea ice models have a nominal 1° resolution.

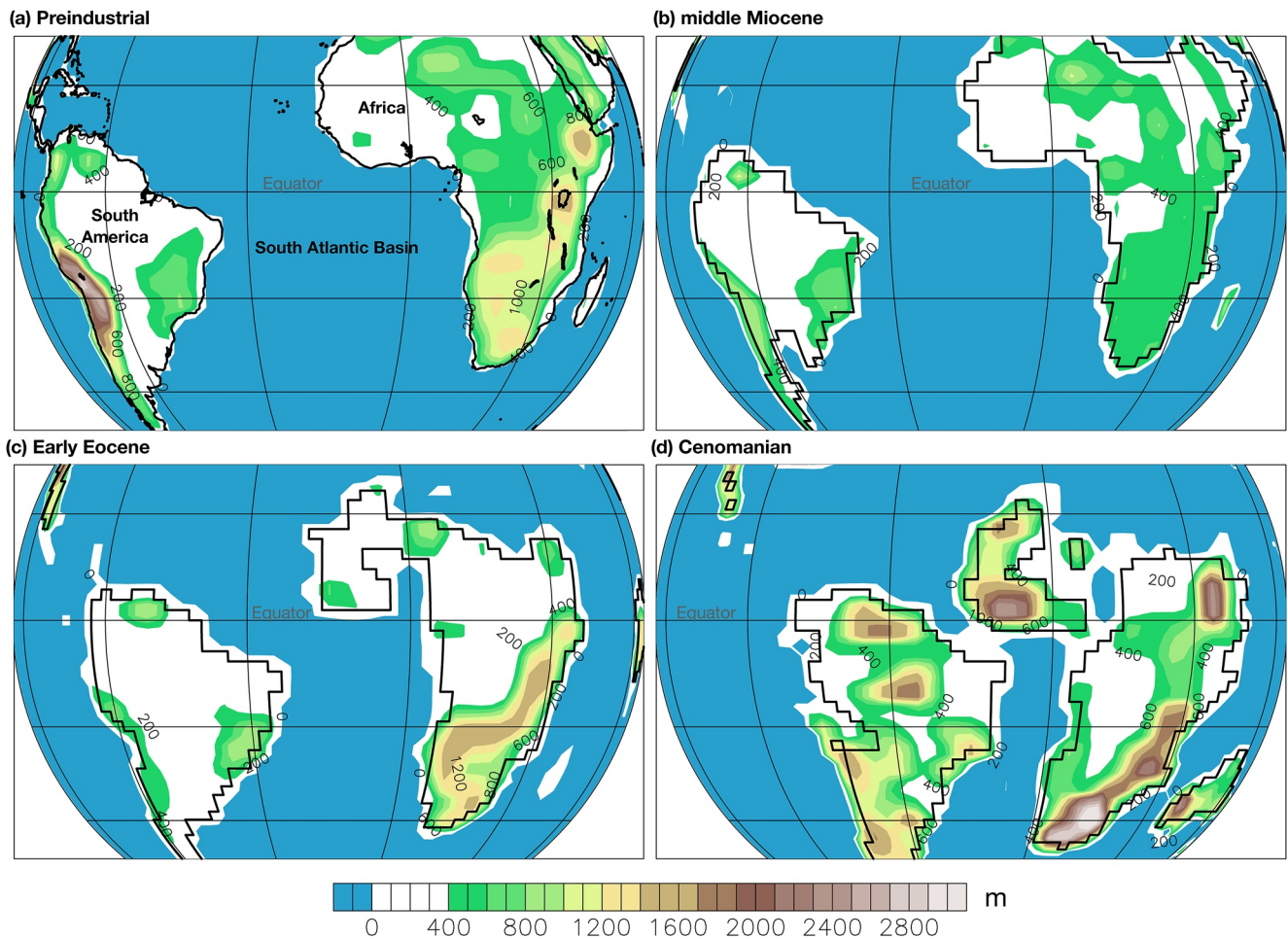


Figure 1. South American and African geography and topography (m) for (a) Preindustrial, (b) middle Miocene (~15 Ma), (c) early Eocene (~55 Ma), and (d) Cenomanian (~90 Ma) simulations.

2.2. Experiments and Boundary Conditions

Four primary CESM1.2 simulations were performed as part of this study. Each was run with age-specific paleogeography and land-surface conditions. Most other boundary conditions were specified with PI values, except as noted, to minimize non-geography-related differences. Our PI simulation is utilized as the modern-day analog. We perform simulations of the middle Miocene, early Eocene, and Cenomanian periods with multiple atmospheric CO_2 levels. To isolate the role of paleogeography, our analysis primarily focuses on the simulations with PI level CO_2 (~280 ppm). Simulations with higher time-specific CO_2 levels (400 ppm for the middle Miocene, 1,700 ppm for the early Eocene, and 1,700 ppm for the Cenomanian) are briefly touched upon. The selected CO_2 levels for the high- CO_2 simulations were based on previous model-data studies (Burls et al., 2021; Goldner et al., 2014; Lunt et al., 2017; Tabor et al., 2016; Zhu et al., 2019). The middle Miocene, early Eocene, and Cenomanian simulations were run for at least 1,500 years to bring the surface climate into steady-state and have a top of the atmosphere energy imbalance of no more than 0.3 W/m^2 . Full equilibration of the deep oceans would likely require several thousand years of additional integration. For detailed information regarding the integration length of simulations and assessment of the equilibrium state, readers are referred to Table S1 in Supporting Information S1 (see also Goldner et al., 2014; Zhu et al., 2019).

The progressive widening of the South Atlantic Basin, northwest movement of the South American continent, and northeast movement of the African continent from the late Cretaceous to the modern-day is illustrated in Figure 1. The width of the South Atlantic Basin at 10°S (Figure 2a) was approximately 25%, 50%, and 90% of the PI value during the Cenomanian, early Eocene, and middle Miocene. The boundary conditions include

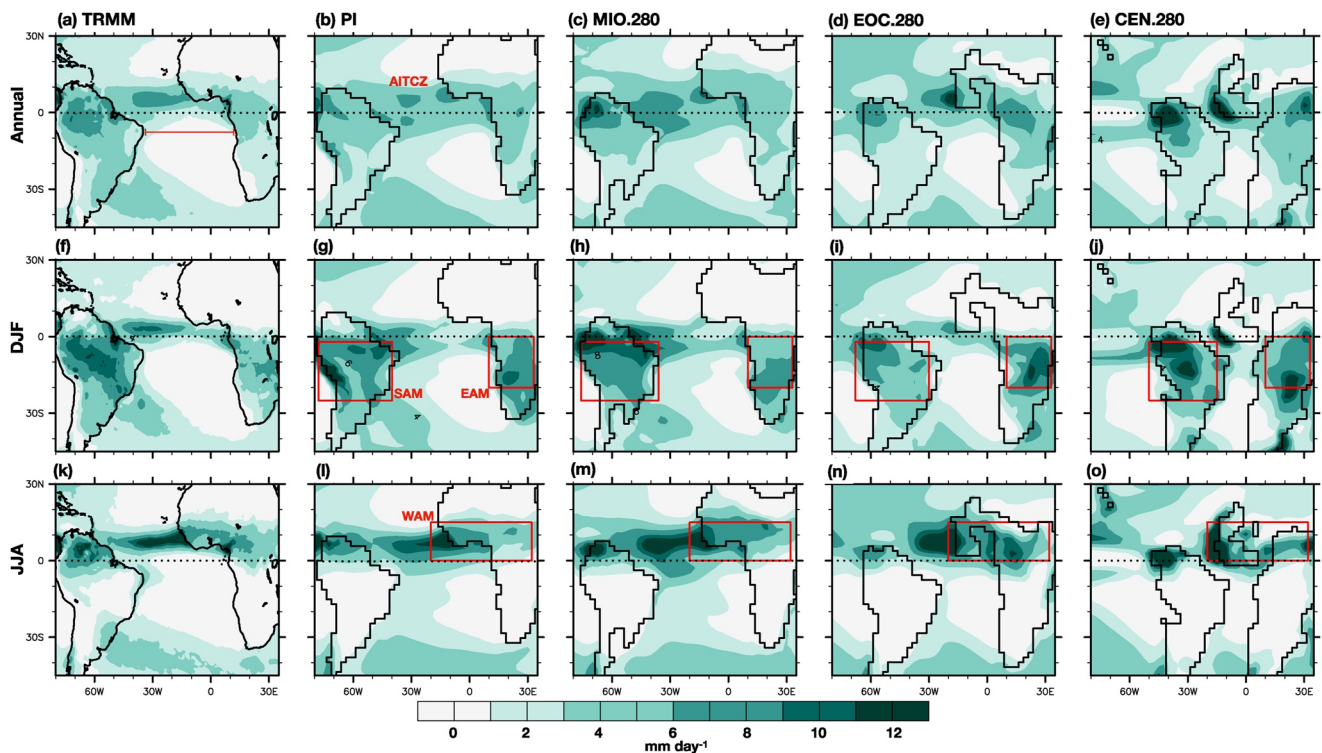


Figure 2. Total precipitation rate (mm day^{-1}) for TRMM (a, f, and k), preindustrial (b, g, and l), MIO.280 (c, h, and m), EOC.280 (d, i, and n), and CEN.280 (e, j, and o). The top row displays the annual mean, the middle row shows the austral summer, and the bottom row shows the boreal summer climatologies. The dashed line represents the equatorial line. The red line across plot (a) represents the longitudinal width across the South Atlantic Basin, where we measured the distance between the South American and African continents. Boxed regions in plots (f) and (k) show the South American, East African, and West African monsoons regions used for Figure 3.

substantial differences in paleotopography that are shown in Figure 1 and highlighted in Table 1. We elaborate on the specific paleoclimate boundary conditions below. For the global paleogeographic distribution, see Figure S1 in Supporting Information S1.

The middle Miocene simulations (MIO) in this study used the boundary conditions that were initialized from the high ice sheet, 400 ppm pCO_2 middle Miocene Climatic Optimum simulation in Goldner et al. (2014), and were published in Gaskell et al. (2022). Unlike CCSM4 in Goldner et al. (2014), we used CESM1.2, which has an updated atmosphere model CAM5 and has been demonstrated to have improved performance for paleoclimate simulations (Zhu et al., 2020). The South American and African vegetation represents tropical moist environmental conditions and is dominated by tropical and temperate forests with grasslands (Figure S4 in Supporting Information S1; Herold et al., 2010). The aerosol prescription was specified as the PI natural aerosol distribution. The simulations use a set of PI orbital parameters with a fixed solar forcing for 1850 CE.

The early Eocene simulations were from the published work of Zhu et al. (2019), which used the published topography and bathymetry boundary conditions of the early Eocene (~ 55 Ma) (Herold et al., 2014; Lunt et al., 2017). South American and African continents consist of a warm and dry vegetation biome with shrubland and desert-dominated ecosystems. The northwest sector of South America and significant parts of the African continent along the equatorial region possess some tropical rainforests but are dominated by shrubland and grassland (Figure S2 in Supporting Information S1; Herold et al., 2014). PI natural aerosols prescriptions were redistributed based on the Eocene paleogeography following the method of Heavens et al. (2012). In this method, the Modal Aerosol Model is used to simulate a prognostic sea salt and dust aerosol distribution based on topography, bathymetry, and land information (vegetation and glaciation). Aerosols such as dimethylsulfide and black carbon were distributed symmetrically between hemispheres using monthly zonal average PI values.

The Cenomanian (~ 95 Ma) simulations used for this study are revised versions from the recently published Community Climate System Model version 4 (CCSM4), Cenomanian simulations (Ladant et al., 2020; Tabor

Table 1
Model Experiments

| Case Name | Ocean Configuration | CO ₂ (ppm) | Dominant South America and Africa vegetation Type | Aerosols | Miscellaneous |
|--------------|---------------------|-----------------------|---|---------------------|--|
| PI | Fully Coupled | 284.7 | Preindustrial | Preindustrial | Simulation from Zhu et al., 2019 |
| MIO.280 | Fully Coupled | 280 | Tropical and evergreen forest Herold et al., 2010 | Preindustrial | Boundary Conditions from Goldner et al., 2014 ran with CESM1.2 CAM5 |
| MIO.400 | Fully Coupled | 400 | Tropical and evergreen forest Herold et al., 2010 | Preindustrial | Boundary Conditions from Goldner et al., 2014 |
| MIO.280.FLAT | Fixed SST | 280 | Tropical and evergreen forest Herold et al., 2010 | Preindustrial | Branched from MIO.280 with South American and African terrain set to 100 meters |
| MIO.280.Sav | Fully Coupled | 280 | Savannah | Preindustrial | Branched from MIO.280 with South American and African vegetation set to savannah |
| EOC.280 | Fully Coupled | 280 | Dry shrubland and desert dominated with small clusters of tropical forest Herold et al., 2014. | Heavens et al. 2012 | Simulation from Zhu et al., 2019 |
| EOC.1700 | Fully Coupled | 1700 | Dry shrubland and desert dominated with small clusters of tropical forest Herold et al., 2014. | Heavens et al. 2012 | Simulation from Zhu et al., 2019 |
| EOC.280.FLAT | Fixed SST | 280 | Dry shrubland and desert dominated with small clusters of tropical forest Herold et al., 2014. | Heavens et al. 2012 | Branched from EOC.280 with South American and African terrain set to 100 meters |
| EOC.280.SST | Fixed SST | 280 | Dry shrubland and desert dominated with small clusters of tropical forest Herold et al., 2014. | Heavens et al. 2012 | Branched from EOC.280 with 2°C added to SSTs found over west equatorial Atlantic Basin |
| EOC.280 Sav | Fully Coupled | 280 | Savannah | Heavens et al. 2012 | Branched from EOC.280 with South American and African vegetation set to savannah |
| CEN.280 | Fully Coupled | 280 | Low latitude forest and dominated by shrubland and savannah Sewall et al., 2007 | Heavens et al. 2012 | Boundary conditions from Ladant et al., 2020 ran with CESM1.2 CAM5 |
| CEN.1700 | Fully Coupled | 1700 | Low latitude forest and dominated by shrubland and savannah Sewall et al., 2007 | Heavens et al. 2012 | Boundary conditions from Ladant et al., 2020 ran with CESM1.2 CAM5 |
| CEN.280.FLAT | Fixed SST | 280 | Low latitude forest and dominated by shrubland and savannah Sewall et al., 2007 | Heavens et al. 2012 | Branched from CEN.280 with South American and African terrain set to 100 meters |

et al., 2016). The Cenomanian boundary conditions are from the proprietary Getech Plc based paleogeography (Lunt et al., 2016; Tabor et al., 2016). We update the CCSM4 Cenomanian simulations using the CESM1.2. Like the Eocene CESM1.2 simulations, aerosols reconstructions use the Heavens et al. (2012) method. The vegetation distribution in South American and African continents consists of a temperate forest in the tropics but is dominated by shrubland and grassland (Figure S2 in Supporting Information S1; Sewall et al., 2007). The Cenomanian simulation accounted for the $\sim 1\%$ decrease in solar irradiance (Ladant et al., 2020), which have been shown to decrease the global mean temperature by 1.8°C (Laugié et al., 2020).

2.3. Diagnostics, Sensitivity Studies, and Limitations

2.3.1. Intertropical Convergence Zone and Monsoon Diagnostics

The ITCZ is typically defined as a band of enhanced tropical convection and precipitation within the axisymmetric overturning circulation of the Northern and Southern Hemisphere Hadley cells where northerly and southerly trade winds converge over the ocean (Geen et al., 2020). Away from the equator, monsoon circulation develops as maximum solar insolation seasonally migrates between hemispheres, resulting in the maximum moist static energy to be located off the equator and a switch from an axisymmetric to an asymmetric overturning circulation (Gadgil, 2018; Privé & Plumb, 2007a). Aside from total precipitation, this study uses the quasi-convective equilibrium framework (Nie et al., 2010) to help identify changes in Atlantic ITCZ, South American, and African monsoon circulations. In this view, regions of deep convection and large-scale ascent cause the atmosphere thermodynamic profile to approach the moist adiabat. ITCZ and monsoon convective regions are identified by the coupling of subcloud (~ 850 mb) and upper-level (~ 200 mb) equivalent potential temperature (θ_e) (Nie et al., 2010) and designates as the region with maximum moist static energy. In addition, total diabatic heating is used to represent precipitation occurring in the atmospheric column and help identify large-scale atmospheric ascent (Wright & Fueglistaler, 2013). Total precipitable water and moisture flux are utilized to identify changes in the atmospheric hydrological cycle. We focus on subcloud θ_e and SST distribution to determine the impact of changing paleogeography on the Atlantic ITCZ, South American, and African monsoons. However, aside from the location of maximum subcloud θ_e , an ITCZ versus monsoon induced convective systems are indistinguishable thus we provide vertical profile analysis of the Hadley cell overturning circulation to further analyze changes in the ITCZ circulation (Figure 2) and we supplement the thermodynamic framework presented in our results with a simplified modern-day monsoon index (Carmichael et al., 2016; Wang & Ding, 2006) to further identify monsoon regions in our paleoclimate simulations (Figure S13 in Supporting Information S1).

2.3.2. Köppen-Geiger Climate Classification

In lieu of a dynamic vegetation model, to quantify changes in the South American and African tropical rainforest extent between the middle Miocene, early Eocene, and Cenomanian, we use the Köppen-Geiger Climate Classification (referred to as KGCC hereafter) (Peel et al., 2007). In KGCC, a tropical rainforest, monsoon, and savannah all maintain temperatures above 18°C during the coldest month (T_{cold}). These three ecosystems are distinguished by their dry month precipitation (P_{dry}): tropical rainforest has greater than 60 mm, monsoon vegetation has rates less than 60 mm but greater than or equal to 100 minus (mean annual precipitation/25), and savannah has P_{dry} less than 60 mm and 100 minus (mean annual precipitation/25).

2.3.3. Additional Sensitivity Studies

We offer complimentary low- CO_2 (280 ppm) fixed SST simulations to explore the sensitivity of our results to orography, coastal SST warming, and vegetation distribution. To understand the role of orography, we performed fixed SST simulations in which the South American and African terrains were set to 100 m (Figures S4 and S5 in Supporting Information S1). We highlight the impact of changes in SST distribution on the Atlantic ITCZ and South American monsoon, using a fixed SST simulation of the early Eocene where the northeastern coast of South America was warmed by 2°C (Figure S9 in Supporting Information S1). We added 2°C warming to the northeastern coast to replicate the coastal warming found in the observations, PI, and middle MIO (Figures 7a–7c). Finally, since the vegetation distribution in our simulations was prescribed, we use fully coupled simulations to test if modifying the South American and African vegetation would impact the South American and African monsoon precipitation distribution. A set of middle Miocene and early Eocene vegetation sensitivity tests were performed where the ecosystem over South America and Africa were set to savannah grassland type (Figures S10 and S11 in Supporting Information S1). A savannah-type ecosystem should represent a generic vegetation type that does

not substantially change the surface albedo compared with an entirely bare ground (desert) or introduce excess evapotranspiration as a fully forested region. We note that fixed SST sensitivity studies used quasi-spun-up SSTs taken from each low-CO₂ fully coupled paleoclimate simulation: MIO.280, ECO.280, and CEN.280.

2.3.4. Limitations

We acknowledge several limitations in our work. Paleogeographic reconstruction of the middle Miocene and early Eocene were based on Müller et al. (2008), while the Cenomanian was based on Markwick and Valdes (2004), which do not use the same reference frames. This lack of self-consistency in plate rotations and paleotopographies, especially between the transition from the Cenomanian to the early Eocene simulation, represents a degree of uncertainty associated with paleoaltimetry and paleocoastlines (Burls et al., 2021; Carmichael et al., 2016; Lunt et al., 2017), and should be further tested in the future as better-constrained paleoclimate reconstructions become available. Nonetheless, for the purpose of our work, we find the expansion of the South Atlantic seafloor to be generally consistent with a progressively widening basin and should not substantially alter our findings. Additionally, our study uses prescribed vegetation rather than an interactive vegetation model (Fisher et al., 2015), which lacks the ability to predict the rapid collapse of plant biomes. Recent work (Tabor et al., 2020) has shown that the addition of grassland or low albedo plant functional types in northern Africa can also increase the northern extent of the African monsoon and impact the precipitation magnitude of the South American monsoon. The sensitivity of the South American and African climate to prescribed vegetation is explored in Figures S10 and S11 in Supporting Information S1. We also note that differences in orbital forcing (Cruz et al., 2009; Goldner et al., 2014), land-ice distributions (Goldner et al., 2013; Singh et al., 2016), and paleo aerosol distribution (Heavens et al., 2012; Zhu et al., 2019) can also impose forcings on the climate system which were not explored in our study.

3. Results

3.1. Simulation of Modern-Day Tropical Precipitation Patterns

To assess how well the CESM1.2 captures the Atlantic ITCZ, South American, and African monsoons, we compare precipitation rates in the PI simulation to satellite observations Tropical Rainfall Measuring Mission (TRMM) (Huffman et al., 2007). The TRMM is based on 12 years of climatology from 1998-to 2009. To simplify our comparison in this section, we define the Atlantic ITCZ as an enhanced zonal precipitation band over the ocean that seasonally migrates between the Northern and Southern Hemisphere subtropical Atlantic Basin or $\sim 10^\circ$ of the equator, while monsoon centers are designated as the location of maximum seasonal precipitation rate over the continent (Figure 2; Geen et al., 2020). The monthly progression of the South American, West African, and East African monsoons are shown as monthly averaged precipitation rates over the boxed regions in Figure 2 (Figure 3).

The comparison between TRMM and PI shows that the PI captures the annual distribution of the Atlantic ITCZ and its seasonal cross hemisphere migration (Figures 2a and 2b). The PI simulation exhibits a double Atlantic ITCZ pattern (Siongco et al., 2015) during the austral summer but not during the boreal summer. Nonetheless, it captures enhanced precipitation rates along the North Atlantic Basin (Figures 2f, 2g, 2k, and 2l). High South American monsoon precipitation rates over the Amazon Basin and orographic precipitation along the front of the Andes are captured by the PI (Figures 2f and 2g). The monthly progression of the South American monsoon in the PI shows a good comparison with TRMM (Figure 3a, lines gray and black). The maximum East African monsoon precipitation location in the PI and TRMM is at $\sim 18^\circ\text{S}$ (Figures 2f and 2g). Compared to TRMM, the monthly progression of the East African monsoon precipitation is well captured by the PI simulation but simulates higher austral summer precipitation rates (Figure 3b, lines gray and black). Compared to TRMM, the PI captures the coastal West African monsoon precipitation but has weaker precipitation rates over central Africa (Figures 2k and 2l). The monthly progression of the West African monsoon is well captured by the PI but shows greater precipitation rates during the peak boreal summer month of July (Figure 3c, lines gray and black). The precipitation comparison between PI and TRMM indicates that CESM1.2 does a reasonable job of capturing the modern-day Atlantic ITCZ, South American, and African monsoons and gives confidence to our paleoclimate simulations.

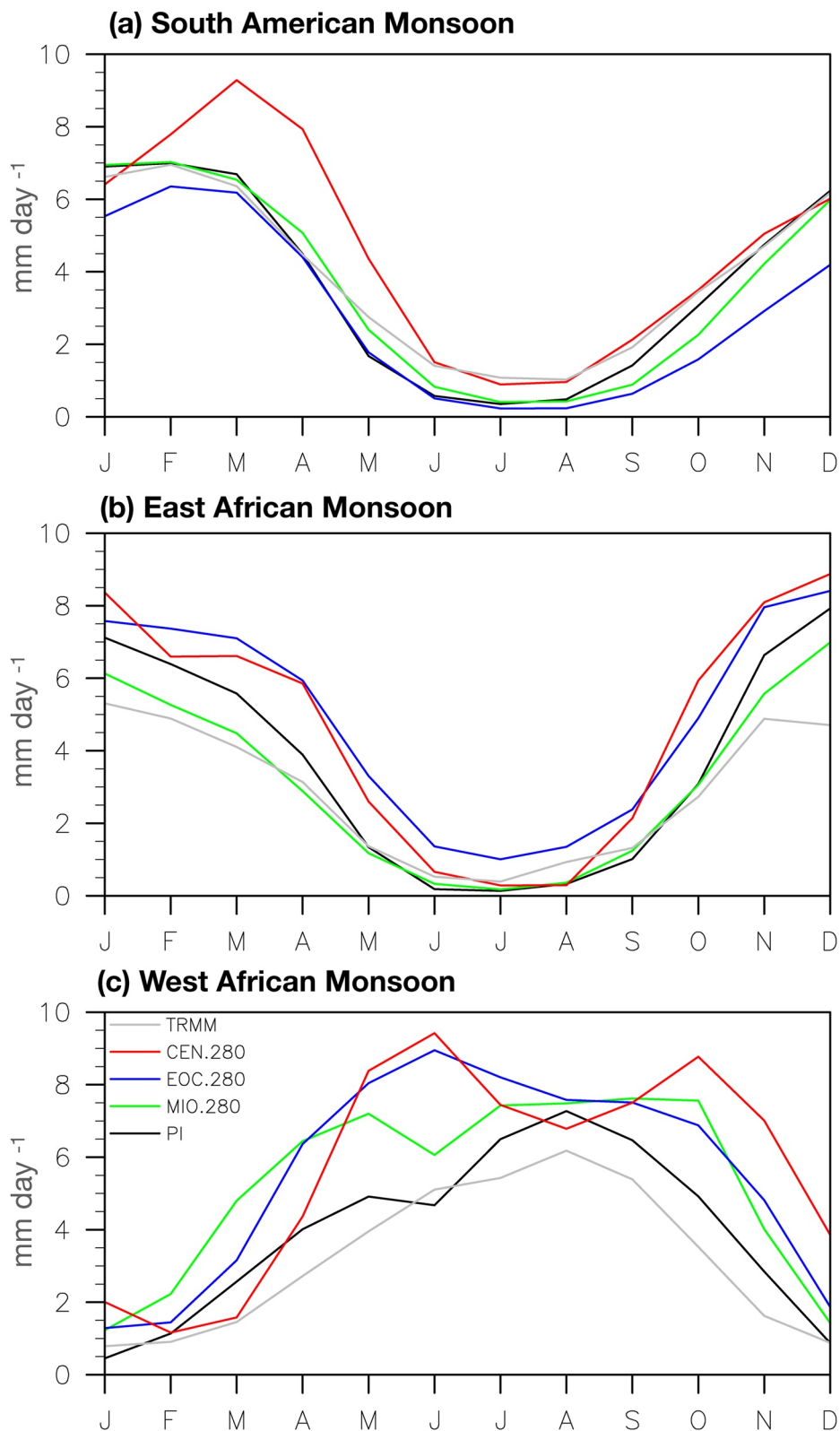


Figure 3. Annual distribution of total precipitation rate (mm day^{-1}) averaged over the monsoon systems found in Figure 1. The monsoonal regions are shown in Figures 2f and 2k and are adjusted appropriately for the paleoclimate simulations.

3.2. Simulation of Tropical Precipitation Patterns Since the Cenomanian

Since the Atlantic Basin was nearly closed in CEN.280 simulation, much of the Atlantic ITCZ precipitation does not exist (see also analysis in Section 3.3.1). Most of the precipitation occurs along the western coast of Africa or within the continental interior of South America and Africa (Figures 2e, 2j, and 2o). In the EOC.280 simulation, weak precipitation occurs over the Northern Hemisphere Atlantic Ocean, associated with the emergence of the Atlantic ITCZ. However, unlike the PI and TRMM, where the precipitation maximum occurs near the eastern coast of South America, the Atlantic ITCZ during the early Eocene is shifted toward the West African coastline (Figures 2d, 2l, and 2n), suggesting that the narrow South Atlantic Basin and the southward location of the African continent during the early Eocene strongly influence its location (see Section 3.3). The Atlantic ITCZ fully forms as the South Atlantic Basin is widened in the MIO.280 simulation. Similar to the PI and TRMM, enhanced precipitation over the eastern coast of South America occurs during the austral summer season (Figure 2h).

The South American monsoon precipitation season duration is approximately the same between the EOC.280, MIO.280, and PI simulations (Figure 3a), while enhanced precipitation rates occur well into the late spring in the CEN.280 simulation extends. In the CEN.280 and EOC.280 simulations, the South American monsoon is centered over the western coast of South America and exhibits lower precipitation over the eastern Amazon Basin than the PI and TRMM (Figures 2i and 2j). Similar to the PI, the MIO.280 exhibits enhanced precipitation over the east Amazon Basin and the eastern coastal region (Figures 2g and 2h). The lack of precipitation over the east Amazon in the simulations when the basin was narrow suggests that the South American monsoon expanded eastward during the late Cenozoic. We further investigate the reason for this expansion in the subsequent section (see Section 3.3.2). However, regardless of the changes in paleogeography, the modern-day monsoon index suggests that in all three periods, the South American Monsoon brings more than 60% of the annual precipitation over the South American continent and 90% percent over the Amazon region (Figure S13 in Supporting Information S1).

In our simulations, the West African monsoon migrates from near the equator ($\sim 1^\circ\text{N}$) in the Cenomanian to the subtropics ($\sim 10^\circ\text{N}$) in the PI. In both the CEN.280 and EOC.280 simulations, boreal precipitation rates are much greater than in the MIO.280, PI, and TRMM cases (Figure 3c). In the paleoclimate simulations, the West African monsoon has an earlier onset around April and diminishes during the end of the boreal summer (Figure 3c). In the MIO.280 case, the West African monsoon circulation is much weaker in magnitude and is stretched east-west across the tropical Atlantic Basin and is similar to those found in the PI case suggesting that the West African monsoon weakened through time (see Section 3.3.3 for further analysis). Regardless of the northward shift of the West African monsoon center, the modern-day monsoon index suggests that the West African Monsoon brings more than 60% of the annual precipitation over the North African continent (Figure S17 in Supporting Information S1). In all three paleoclimate cases, the East African monsoon resides near 15°S and is stronger during the early Eocene and Cenomanian. The modern-day monsoon index suggests that in all three periods, the East African Monsoon brings more than 60% of the annual precipitation over the South African continent (Figure S13 in Supporting Information S1). Since the East African monsoon location remains relatively stationary between our paleoclimate simulations but does change in magnitude, we suspect that different topographic configurations could influence our results (see Section 3.5 for further analysis).

3.3. Role of Continental Drift on the Development of Tropical Precipitation

3.3.1. Development of the Atlantic Intertropical Convergence Zone

To understand the impact of paleogeography on the development of the Atlantic ITCZ, we examine the evolution of the Hadley cell over the Atlantic region. The region of maximum vertical velocities aligns with the region of maximum subcloud θ_e , upper-level θ_e , diabatic heating, and precipitation rate, which represents the ascending branch of the Hadley cell circulation (Figure 4). In the PI case, annual surface temperature and precipitation peaks near the equatorial Atlantic (Figure 4a). The PI simulation shows two axisymmetric overturning circulations with maximum annual θ_e and diabatic heating at the center. Spatially, the maximum annual subcloud and upper-level θ_e are located over central South America and Africa but expand across the tropical Atlantic Ocean (Figure S3 in Supporting Information S1).

Changes in South Atlantic Basin width cause the regional surface and atmospheric thermodynamic profile and overturning circulation to differ. In the near absence of a South Atlantic Basin, the CEN.280 case exhibits a strong Northern Hemisphere overturning circulation with maximum subcloud, upper-level θ_e , and diabatic heating

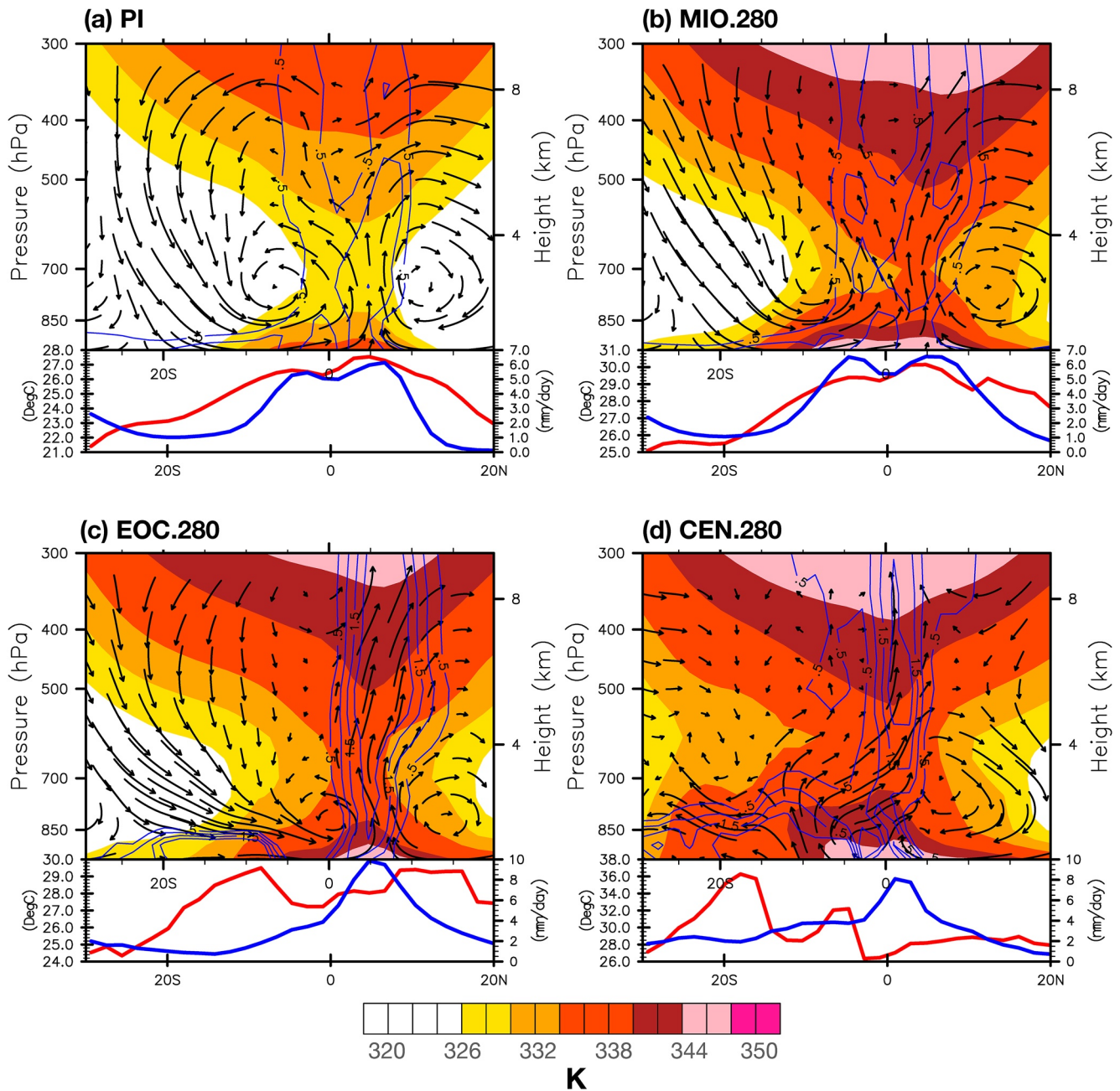


Figure 4. Annual zonal average θ_e (K; color shadings) in pressure coordinates overlain with maximum total diabatic heating (K day^{-1} ; light-blue contours lines) in pressure coordinates. Vectors are ω (Pa day^{-1}) scaled with meridional winds (m s^{-1}) with the reference vector of one. The attached plots show zonal average surface temperature (K, red line) and total precipitation rate (mm/day, blue line). All variables were averaged over 15°W and 30°W . The simulations presented are preindustrial, MIO.280, EOC.280, and CEN.280.

collocated with the ascending branch of the Hadley cell ($\sim 5^\circ\text{N}$) (Figure 4d). The Southern Hemisphere overturning circulation, a feature of the modern-day Atlantic ITCZ, is not present in the CEN.280 simulation (Figure 4d). In this case, the South American and African continents have enhanced subcloud θ_e over the west coast of South America and Africa (Figure S3 in Supporting Information S1), which divert precipitation toward the interior of the continents rather than over the Atlantic Ocean (Figure 2e). In the EOC.280 simulation, southerly low-level winds associated with weak Southern Hemisphere trade winds (Figure S7 in Supporting Information S1) begin to converge toward the region of maximum subcloud, upper-level θ_e , and diabatic heating located north of the equator at $\sim 5^\circ\text{N}$ (Figure 4c). Additionally, a shallow overturning circulation at $\sim 1^\circ\text{N}$ (Figure 4c) and weak

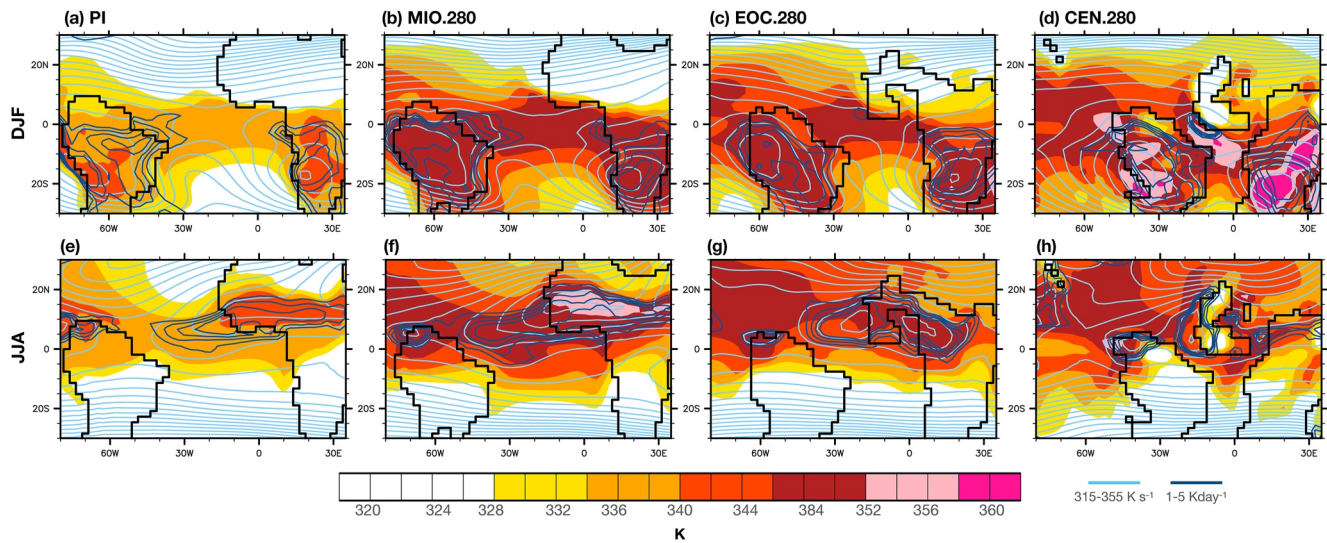


Figure 5. Average subcloud θ_e (850 mb) (K; color shadings) in terrain-following coordinates overlain with upper-level θ_e (315–355 K; 200 mb; light blue contours lines) and maximum total diabatic heating (1,000–100 mb) (1–4 K/day; dark blue contours lines) in pressure coordinates. Plots (a–d) show austral summer (December–February) climatology, and plots (e–h) show boreal summer (June–August) climatology. The simulations presented are preindustrial, MIO.280, EOC.280, and CEN.280.

precipitation (Figure 2d) over the ocean appear in the EOC.280 simulation. As the South Atlantic Basin nears its modern-day width (MIO.280), the maximum subcloud and upper-level θ_e are spread across both hemispheres with maximum precipitation, diabatic heating, and vertical velocities located along the equator (Figures 4a and 4b). Notably, a shallow (1,000–500 mb) overturning circulation at $\sim 7^\circ\text{S}$, separate from the large-scale subsidence at $\sim 20^\circ\text{S}$, forms in the Southern Hemisphere. As in the PI, the MIO.280 simulation shows the formation of Southern Hemisphere trade winds (Figure S7 in Supporting Information S1) and the maximum annual precipitation rates occurring between 5°S and 5°N (Figure 4b, blue line).

Our simulations indicate that basin width substantially controls the origin and development of the Atlantic ITCZ. The insufficient body of water found over the South Atlantic Basin during the Cenomanian inhibits the formation of a Southern Hemisphere overturning circulation. The substantially closer South American and African continents concentrate the annual mean precipitation toward the continental interior rather than over the ocean. Although the exact period is unknown, the early Eocene represents a transition scenario between the modern-day and the Cenomanian. In this case, the South Atlantic Basin was still narrow but had sufficient fetch for southerly low-level winds and convection to occur over the Atlantic Ocean. We find the Northern Hemisphere overturning circulation persisting since the formation of the Northern Atlantic Basin (Poblete et al., 2021; Seton et al., 2012). Our study demonstrates that a Southern Hemisphere Hadley cell overturning circulation fully existed in the Miocene, but we hypothesize that this could have occurred earlier as the South Atlantic Basin gained a sufficient fetch (Poblete et al., 2021; Seton et al., 2012).

3.3.2. Development of the South American Monsoon

In this section, we identify the role of widening the South Atlantic Basin and the northward movement of South America in the development of the South American monsoon. In the CEN.280 and EOC.280 simulations, maximum subcloud θ_e that is coupled to the upper-level θ_e is isolated over western South America, which leads to a concentration of total precipitable water over this region (Figures 5c, 5d, 6c, and 6d). In the EOC.280 simulation, the maximum subcloud θ_e over western South America does not connect with the subcloud θ_e over the equatorial Atlantic Basin, which is supported by the lack of diabatic and precipitable water over the northeastern coast of South America (Figures 5c, 5d, 6c, and 6d). With the widening of the South Atlantic Basin, the MIO.280 and PI simulations exhibit enhanced subcloud and upper-level θ_e that coincide with enhanced diabatic heating and precipitable water extending from western South America, across the Amazon Basin and terminating at the northeastern coastal region of South American (Figures 5a, 5b, 6a, and 6b). In sum, the simulations suggest that the widening of the Atlantic results in South American monsoon precipitation expansion over the east Amazon basin.

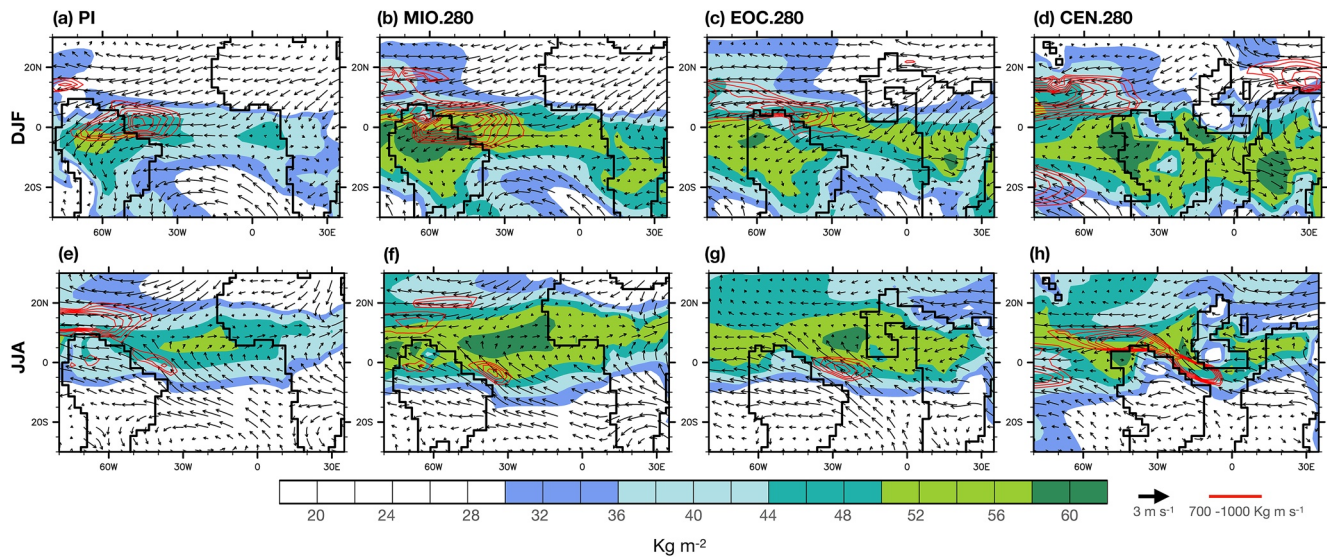


Figure 6. Vertically integrated total precipitable water (kg m^{-2} , color contours), overlain with maximum vertically integrated (1,000–100 mb) moisture flux magnitude (kg m s^{-1} , red contour lines) and surface (850 mb) winds (m s^{-1} , vectors) in pressure coordinates. Plots (a–d) show austral summer (December–February) climatology and plots (e–h) show boreal summer (June–August) climatology. The simulations presented are preindustrial, MIO.280, EOC.280, and CEN.280.

To explain how paleogeography impacts the formation of convective systems over the Amazon Basin, we show atmospheric moisture flux, SSTs, and currents distribution. In the CEN.280, easterly winds entering South America are weak. Instead, a westerly flow from the Pacific Basin supplies moisture toward western South America (Figure 6a vs. Figures 6d and S6 in Supporting Information S1). In the EOC.280, low-level winds and maximum moisture flux originate from northeasterly flow, suggesting a transition to a modern-like surface wind or trade winds-like distribution. Further widening of the South Atlantic Basin and northward migration of the South American continent in the MIO.280 strengthens easterly moisture flux to the continental interior. A full Atlantic easterly trade wind is established in the MIO.280 simulation (Figure S7 in Supporting Information S1). Moisture flux analysis suggests that the additional fetch over the Atlantic Basin and northward location of the South American continent increased the amount of moisture transported into the continental interior (Figure 6c vs. Figure 6b; Liu et al., 2019).

Changes in regional ocean circulation due to paleogeography also impacted the South American monsoon. As in World Ocean Atlas (WOA), the PI shows warm SSTs along the tropical west coast of Africa and the tropical eastern coast of South America. In the CEN.280 case, South Atlantic Basin SSTs are substantially warmer than the modern and paleoclimate cases due to the narrowness and shallowness of the basin (Figure 7e). In the EOC.280 case, warm SSTs form over the tropical west coast of Africa. However, due to the weaker Southern Hemisphere easterly trade winds (Figures 7d and S7 in Supporting Information S1), warm SSTs over the tropical eastern coast of South America do not form. Since the Southern Hemisphere easterly trade winds are fully developed in the MIO.280 case, warm SSTs over the northeastern coast of South America begin to form (Figures 7b, 7c, and S7 in Supporting Information S1). The formation of warm SSTs found over the eastern coast of South America in the MIO.280 and PI simulations coincide with enhanced easterly moisture flux, the maximum subcloud and upper-level θ_e , and diabatic heating (Figures 5a, 5b, 7b, and 7c). The coevolution of warm SSTs and convective systems over the northeastern coast of South America suggests that well-developed easterly trade winds, which are not found in the Cenomanian and early Eocene cases when the basin was narrow, are necessary for the South American monsoon precipitation to migrate eastward.

3.3.3. Development of the East and West African Monsoons

In Section 3.2, we showed that the East African monsoon precipitation remains near 15°S in all cases. The maximum East African monsoon subcloud θ_e coupled to the upper-level θ_e is centered at 15°S in all four cases, with the CEN.280 with the warmest subcloud θ_e distribution (Figure 5). Moisture flux analysis in the CEN.280 and EOC.280 indicates that most of the precipitable water is delivered by westerly onshore flow from the South Atlantic Basin and by northeasterly flow from the Tethys seaway (Figures 3b, 6c.). In the MIO.280 and PI

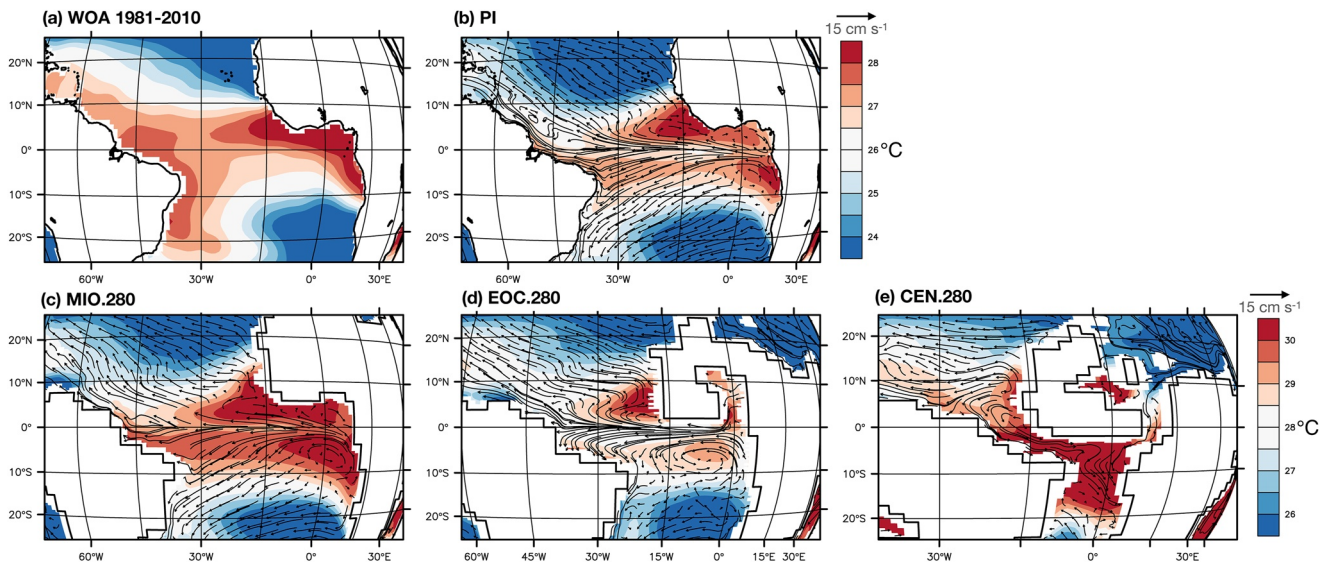


Figure 7. Austral summer (December–February) sea surface temperatures (SSTs) ($^{\circ}\text{C}$) overlain with surface currents (cm s^{-1}). Plots show the World Ocean Atlas 2018 (Boyer et al., 2018) averaged over 1981–2010 (a), and CESM1.2 simulations: preindustrial (b), MIO.280 (c), EOC.280 (c), and CEN.280 (e). SST values show adjusted values for the modern (a, b) and paleoclimate (c–e) cases.

simulations, with the emergence of the northern African landmass and closure of the Tethys Sea, an increased flux of northerly dry air weakens the East African monsoon, making the South Atlantic Basin the primary source of moisture (Figures 6a and 6b). Warm SSTs found over the Gulf of Guinea during the austral summer remained stationary since the late Cretaceous (Figures 6 and 7). Notably, differences in the East African Plateau elevation, which vary dramatically between our simulations, influence the poleward extent and the magnitude of the East African monsoon precipitation (Section 3.6).

Unlike the East African monsoon, the West African monsoon strength in all four simulations is connected to the location of the western coast of West Africa, which drifted away from the equator and South American continent through time. The maximum West African monsoon subcloud θ_e coupled to the upper-level θ_e is centered at $\sim 5^{\circ}\text{N}$ in the CEN.280, $\sim 10^{\circ}\text{N}$ in the EOC.280, and at $\sim 15^{\circ}\text{N}$ in the MIO.280 (Figure 5). Monsoon diagnostics indicate that the West African monsoon center in the CEN.280 and EOC.280 was located near the equator (Figures 5g and 5h) and drifted toward the subtropics in the MIO.280 case (Figure 5f). With West Africa closer to the equator in the CEN.280 and EOC.280 cases, warm surface temperatures over land and adjacent bodies of water (not shown) enhance convection over the region (Figures 2n and 2o). Additionally, a narrow South Atlantic Basin in the CEN.280 and EOC.280 allows strong cross-equatorial flow off the coast of South America to directly deliver moisture into the West African monsoon, further strengthening the circulation in these cases (Figures 6g and 6h). However, the northward movement of Africa in the MIO.280 and PI cases shifted the circulation toward the subtropics, effectively weakening the thermally driven circulation and increasing its seasonality. At the same time, as the South Atlantic Basin widened, the strong southerly cross-equatorial flow is redistributed along the entire tropical Atlantic Basin, decreasing the moisture flux into the West African monsoon circulation (Figures 6e and 6f). Since much of the Northern Atlantic Basin was already open during the late Cretaceous, our results indicate that changes in ocean circulation due to the North Atlantic Basin had a much smaller influence on the West African monsoon. In support, seasonally warm SSTs coinciding with the West African monsoon precipitation center over the coast of West Africa appear in all cases (10°N) (Figure 8).

3.4. Elevated CO_2 Levels Versus Paleogeography

Increasing CO_2 concentrations leads to increased land and ocean surface temperatures in our paleoclimate simulations (Figure 9 and S8 in Supporting Information S1). Increased temperature enhances the already established Atlantic ITCZ, South American, and African monsoon precipitation. We find that increasing CO_2 concentrations do not reorganize precipitation regimes but can primarily strengthen them (Figure 9 vs. Figure 1). For example, as in the CEN.280, the monsoon centers remain constant in the CEN.1700 (Figures 1e and 9c). As in the EOC.280,

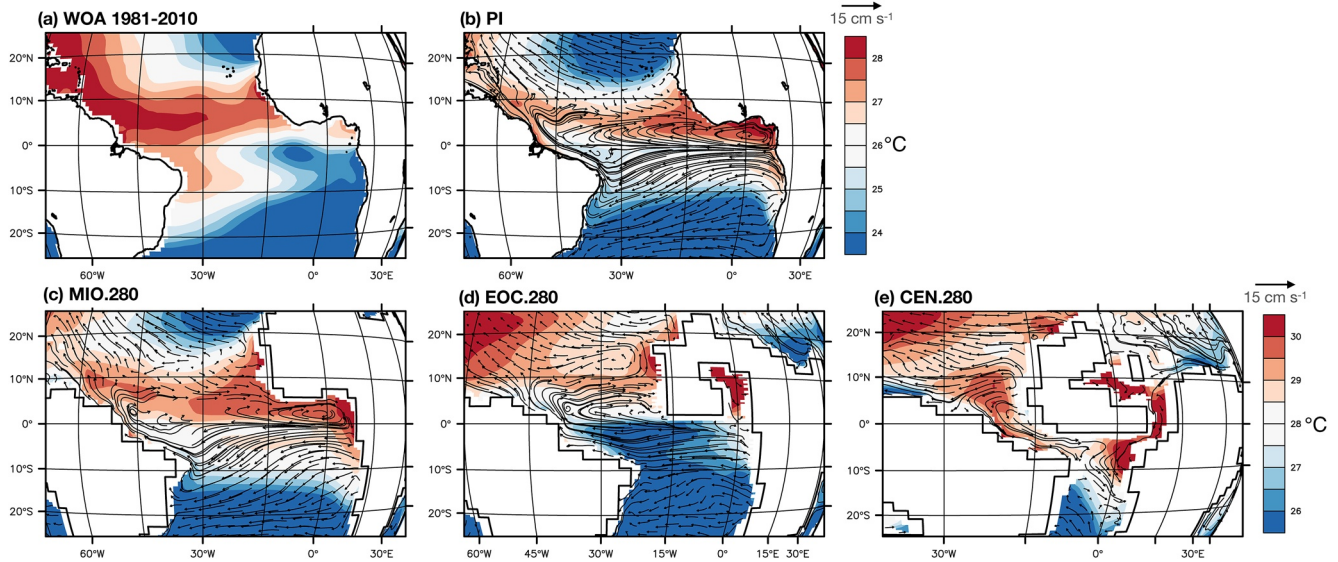


Figure 8. Caption the same as Figure 7 but for boreal summer months (June–August).

maximum Atlantic ITCZ precipitation is located off the western coast of West Africa in EOC.1700 (Figures 9b, 9e, and 9h). In MIO.400, the location of the precipitation center for the Atlantic ITCZ, South American, and African monsoons remain the same as we increase CO₂ concentrations (Figures 9a, 9d, and 9g). Our simulations produce an increased precipitation rate in the subtropics at higher CO₂ levels but only in regions where precipitation is already established.

3.5. Topography Versus Continental Drift

To determine if topography strongly impacts the resulting Atlantic ITCZ, South American, and African monsoon precipitation distribution, we provide several topography sensitivity simulations where South America and Africa terrain was flattened. We find that topography enhances tropical precipitation; however, continental drift has a first-order control on how tropical precipitation is organized. For example, in the CEN.280 case, regions of elevated topographies in northern South America and Africa (Figure 1d) coincide with the location of maximum precipitation rates (Figure 2j). Removal of the high topography lowers the South American monsoon and West African monsoon precipitation over northern South America and Africa but does not remove the associated northwestern South American and African precipitation (Figures S4c, S4f, S5c, and S5f in Supporting Information S1). Topography, however, influence the poleward organization of precipitation because it can redistribute where the maximum subcloud θ_e and orographic precipitation reside (Figures 2g and 5a). For example, the Andes topography is low or absent in all the paleoclimate cases. In these cases, southward moisture transport along the Andes, as occurs in the PI via a low-level jet (Insel et al., 2010; Poulsen et al., 2010), is reduced, allowing the maximum subcloud θ_e to be broadly distributed across South America and precipitation is instead focused over northwest South America (Figure S4 in Supporting Information S1). Additionally, flattening the East African Plateau in EOC.280 and CEN.280 disorganizes the East African monsoon precipitation across Central Africa rather than concentrating over the mountains (Figures S4c and S4f in Supporting Information S1). The continental distribution strongly controls organized rainfall in the tropics since the regional SST distribution influences the mean zonal wind patterns, but the regional topographies strongly control organized precipitation found in the subtropics since it can redirect the transport of moisture and energy (Acosta & Huber, 2020; Geen et al., 2020; Lutsko et al., 2019).

3.6. Changes in South American and African Rainforests

By using the KGCC criteria, we characterized the potential spatial extent of the South American and African tropical rainforest, monsoon, and savannah ecosystems through time. We plot the KGCC criteria for the PI case similarly to Peel et al. (2007) to validate our CESM1.2 simulations (Figure 10a). The PI case shows the eastern

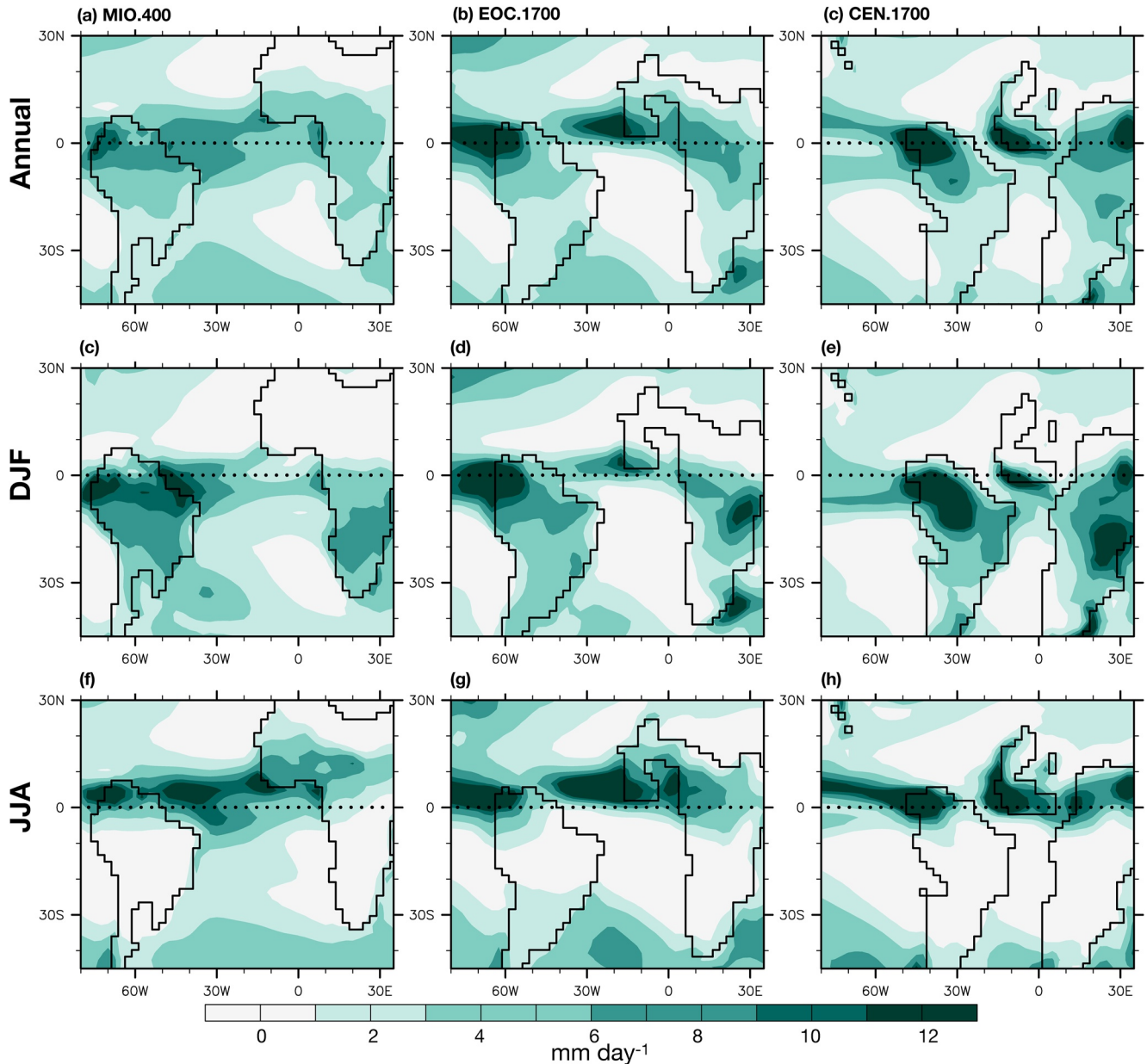


Figure 9. Caption same as Figure 2, but for high CO₂ middle Miocene, early Eocene, and Cenomanian cases.

Amazonian rainforest and the equatorial rainforest in Africa (Figure 10a). The latitudinal extent of the Amazonian monsoon-type rainforest spans from 5°N to 5°S, while the tropical savannah type spans from 10°N to 25°S. Much of the monsoon-type rainforest in Africa is restricted along the equator, while the savannah-type spans from 20°N to 10°S.

The CEN.280 and EOC.280 simulations support the existence of rainforest and monsoon-type ecosystems in northwestern South America and across Central Africa (Figures 10c and 10d), with their poleward extent increasing when CO₂ levels are raised (Figures 10f and 10g). Widening the South Atlantic Basin in the MIO.280 simulation leads to an eastward expansion of the Amazon Rainforest (Figure 10b). A modest increase in CO₂ levels from 280 to 400 ppm during the middle Miocene does not substantially alter the poleward extent of the Amazon Rainforest (Figure 10e). The African rainforest and monsoon-type ecosystem in the middle Miocene remain along the equator but are substantially smaller than those found in the CEN.280 and EOC.280, especially when compared

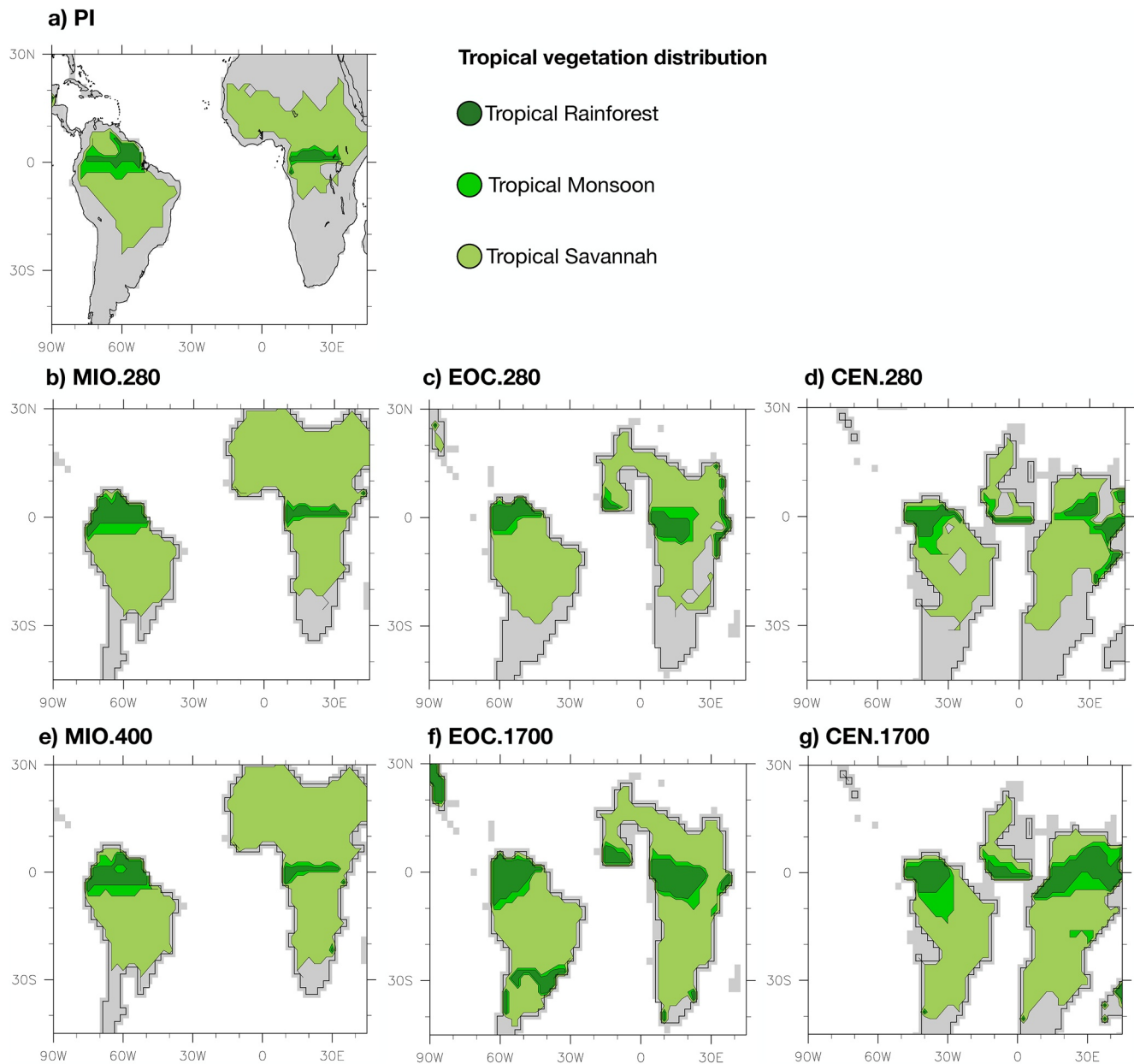


Figure 10. South American and African tropical vegetation distribution was calculated from the Köppen-Geiger climate classification. The simulations presented are preindustrial, MIO.280, EOC.280, CEN.280, MIO.400, EOC.1700, and CEN.1700.

to the higher CO₂ cases (Figures 10e–10g). In all four cases, the savannah ecosystem could have covered much of South America and Africa and expanded poleward with higher CO₂ levels.

4. Discussion

Our simulations reveal the critical role of South American and African continental drift on the Atlantic ITCZ, South American, and African monsoons. For example, in our Cenomanian simulations when the South Atlantic Basin was narrow, and the South American and African continents were located further south than modern-day, the Southern Hemisphere branch of the Atlantic ITCZ was non-existent or weak since the formation of the Southern Hemisphere overturning circulation was hindered by the lack of ocean surface. However, the breakup of the Gondwana “mega-monsoon” (Kutzbach & Gallimore, 1989; Peyser & Poulsen, 2008) is featured by the

Cenomanian simulation where regional South American and African monsoons began development. The early Eocene simulations represent a transitional period where the South Atlantic Basin had sufficient fetch to allow cross-equatorial flow to enhance the West African monsoon but did not allow strong easterly trade winds during the austral summer months to strengthen the South American monsoon (Liu et al., 2019). The middle MIO resembled the modern-day since 90% of the South Atlantic Basin was open. In this case, the Atlantic ITCZ and Southern Hemisphere easterly trade winds were fully developed.

Paleotopography impacted the development and location of the South American and African monsoon precipitation centers. For example, the Cenomanian simulations exhibit large terrains over South America and West Africa not present in any other paleo reconstructions. Removal of such high topographies in South America shows the austral summer precipitation center is generally located in the northwestern sector of South America but would be extended southward if the Andes were present (Figures 1b and S4 in Supporting Information S1). We find changes in topography strongly influence local moisture distribution, and the region of maximum subcloud θ_e , which ultimately reorganizes monsoon centers (Acosta & Huber, 2020; Nie et al., 2010). More recent paleotopographic reconstructions of the Andes suggest that an elevated proto-Andes were already elevated during the Eocene (Boschman, 2021; Canavan et al., 2014; Fiorella et al., 2015), which is not accurately represented in our early Eocene and middle MIO. Nonetheless, without the elevated Andes, precipitation along the eastern Amazon region occurs in our middle Miocene simulation, suggesting that continental drift, and not the rise of the Andes, was responsible for the eastward expansion of the Amazonian rainforest. However, the poleward extent of the South American monsoon is strongly tied to the presence of the Andes (PI simulation, Poulsen et al., 2010). We note that the location of the East African Rift Zone, which varied between our simulations, controls the location of maximum austral summer precipitation over Southern Africa. Precipitation becomes less concentrated without the elevated East African Rift Zone (S4). Our work here demonstrates that the uplift of the Andes (Garzzone et al., 2017; Poulsen et al., 2010) and the East African Rift Zone (Jung et al., 2016; Wichura et al., 2015) can increase the South American and East African monsoon precipitation magnitude and alter the poleward location of the subtropical monsoon centers; thus an extended focused investigation of the elevated Andes or East African Rift Zone across the Cenozoic should be further tested.

Atmospheric CO₂ concentrations have decreased from well above 1,000 ppm in the late Cretaceous to as low as 280 ppm during the PI (Foster et al., 2017), which has substantial implications on the atmospheric hydrological cycle (Burls & Fedorov, 2017; Frierson et al., 2007; Held & Soden, 2006; Huber & Caballero, 2011; Poulsen & Jeffery, 2011; Scheff et al., 2017). Increasing CO₂ is intrinsically tied to the overall warmer land surface and SSTs. Our simulations show that the elevated atmospheric CO₂ levels during the Cenomanian, early Eocene, and middle Miocene strengthened the Atlantic ITCZ, South American, and African monsoon precipitation rate and moisture flux convergence into the continents (Figures 9, and S6 in Supporting Information S1). However, increasing CO₂ does not substantially modify the locality of the monsoon precipitation centers (Figure 9). For example, in EOC.1700 simulation, the South American monsoon precipitation found on the northwestern coast was higher than the EOC.280, but the northeastern coast of South America remained relatively dry. Parts of the South American and African subtropics receive more precipitation under warmer climate conditions (Burls & Fedorov, 2017), which is reflected by our KGCC vegetation classification. However, enhanced precipitation rates due to CO₂ only occur in regions where convective systems are already established, which are determined by paleogeography.

We find that large-scale changes in the location of monsoon centers are primarily contingent on the paleogeography, which can change oceanic and atmospheric large-scale circulation (Farnsworth et al., 2019), while fluctuation in CO₂ mainly enhances the already established precipitation centers. We note that due to differences in boundary conditions (paleogeography, vegetation, soil, ice sheet, or aerosol distribution), the 280 ppm CO₂ paleoclimate simulations were warmer than the PI case (Figure S12a in Supporting Information S1) with the global mean surface temperature (GMST) of the PI, MIO.280, EOC.280, and CEN.280 being ~14, ~19, ~19, and ~20°C, respectively. Such warming due to boundary conditions generally increased zonal mean precipitation rates in the tropics except for the middle Miocene simulation (Figure S12b in Supporting Information S1). The weaker tropical precipitation rate in the MIO.280 is contrasted by enhanced precipitation in the subtropics suggesting an increase in the export of moisture and energy from the equator toward the poles (not shown). Furthermore, increased CO₂ in the simulations MIO.400, EOC.1700, and CEN.1700 resulted in the GMST of ~20, ~30, and ~31°C, respectively. The substantially warmer GMST in the CEN.1700 and EOC.1700 cases

increase precipitation in the tropics suggesting a more enhanced ITCZ during the late Cretaceous and early Cenozoic versus the late Cenozoic where precipitation is greater in the subtropical monsoon regions (Figure S12b in Supporting Information S1).

Our results demonstrate that the influence of continental drift was complex and had a substantial impact on the atmospheric and oceanic circulation. For example, the widening of the South Atlantic Basin not only enhances the onshore moisture flux (Liu et al., 2019) but also forms warm SSTs over the northeastern coastal region of South America. Enhanced moisture flux and warm coastal SSTs coincide with enhanced precipitation over the Amazon Basin. Early Eocene SST sensitivity experiment shows that intense northeastern Amazonian precipitation rates can be reproduced without the enhanced increased onshore moisture flux, given that warm coastal SSTs are present (Figure S9 in Supporting Information S1), which naturally occurs with continental drift. Such a simple SST sensitivity test presented here further emphasizes the role of ocean-atmosphere interactions in controlling the various monsoon circulation (Acosta & Huber, 2020; Lutsko et al., 2019). Additionally, changes in global ocean circulation due to increased CO₂ levels such as the variability in the Atlantic meridional overturning circulation strength (Lynch-Stieglitz, 2017), El Niño-Southern Oscillation (Goldner et al., 2011), and Atlantic upwelling regions (Richter & Xie, 2008) represent avenues that require further investigation. As shown here, the distribution of tropical Atlantic SSTs is essential to the formation of the Atlantic ITCZ (Figures 7 and 8); thus, changes in AMOC circulation, which is known for transporting heat away from the equator, should be further tested but is beyond the scope of our work.

Using the KGCC criteria, we demonstrate that changes in tropical monsoon strength through time most likely altered the vegetation distribution over South America and Africa. The enhancement of the West African monsoon during the Cenomanian to the early Eocene supports the existence of a thriving Pan-African rainforest. However, the South American monsoon was restricted toward the northwestern corner of South America (Jaramillo et al., 2010), effectively drying the eastern Amazonian region (Figures 10f and 10g). As the South Atlantic Basin widened, the South American monsoon began to extend eastward and aided in the west-to-east expansion of the Amazon Forest during the Neogene (Figures 10a, 10b, and 10e). Weakening of the West African monsoon circulation over time leads to a decreased African rainforest extent. The changes in South American and African monsoon strength and locality over time bolster the hypothesis that the decline of the Pan-African rainforests coincided with the growth of the Amazonian rainforests during the Neogene (Jaramillo et al., 2010; Morley, 2011). We demonstrate that the decline of the African rainforest was due to paleogeography and Cenozoic-CO₂ decline. In contrast, the primary mechanism controlling the Amazon rainforest's eastward expansion was paleogeography rather than CO₂ (Liu et al., 2019). We note that the KGCC criteria are calibrated for modern-day vegetation, and plant adaptations could have substantially differed in the past, allowing them to exist in different environments (Carvalho et al., 2021; Morley, 2011). For example, the KGCC criteria only consider T_{cold} and do not consider an upper bound in surface temperatures (Sullivan et al., 2020), which can reach as warm as ~50°C mean annual temperature in both EOC.1700 and CEN.1700 cases. The addition of paleo plant (Richey et al., 2021) functional types and a dynamic vegetation module (Fisher et al., 2015) in future climate model iterations should further improve the work presented here. Nonetheless, although vegetation in our original paleoclimate simulations is fixed, changing the vegetation in our simulations (Figures S10 and S11 in Supporting Information S1) only increases the precipitation magnitude but does not modify the monsoon precipitation centers suggesting that the hydroclimate is primarily controlled by the continental configuration, regional topography, and CO₂ rather than the already established vegetation.

5. Summary

This study presents paleoclimate simulations of the Cenomanian (~95 Ma), early Eocene (~55 Ma), middle Miocene (~15 Ma), and PI (modern-day) using the CESM1.2. We demonstrated that changes in paleogeography associated with the widening of the South Atlantic Basin, northward movement of the South American and African continents, and uplift of the Andes and East African rift zone altered the Atlantic ITCZ, South American, and African monsoons. Our results indicate that changes in CO₂ levels and vegetation distribution play a secondary role to paleogeography. Lastly, using simple precipitation-temperature criteria, our work demonstrates that a western Amazonian and Pan-African rainforest thrived during the late Cretaceous and early Cenozoic. Changes in paleogeography (widening of the South Atlantic Basin and uplift of various mountain ranges) and CO₂ level

decline in the late Cenozoic resulted in the contraction of the Pan-African rainforest and an expansion of the Amazon rainforest.

Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

Data Availability Statement

Datasets for this research are found at the University of Michigan, Deep Blue Repositories (Acosta, 2021). The datasets are available in NetCDF format.

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