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Intermittent development of forest corridors in northeastern Brazil during the last deglaciation: Climatic and ecologic evidence

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ABSTRACT

The semi-arid northeastern (NE) Brazil vegetation is largely dominated by Caatinga, one of the largest and richest dry forests in the world. Caatinga is a strategic biome, since it has borders with Cerrado, Atlantic forests and the Amazon, acting as a potential corridor (or barrier) for biotic interchange between these regions during evolutionary times. Therefore, accurate reconstructions of past vegetation, ecological and hydrological changes in this area are critical to understanding the dynamics of biome boundaries that may play an important role in dispersal and diversification mechanisms and, more specifically, the link between the long-term climate variability and tropical biodiversity. Here, we present high-resolution palynological and elemental data from marine core GeoB16205-4 retrieved off the Parnaíba River mouth (NE Brazil) mainly covering the Younger Dryas (YD). We show that the YD interval was predominantly wet in NE Brazil, yet it was not homogenous and two distinct phases could be distinguished. A marked intensification of wet conditions between ~12.3 and 11.6 cal kyr BP was recorded by the expansion of tropical rainforest and tree ferns. These results are in agreement with the transient TraCE-21k coupled climate model simulation. We infer that the second pluvial phase of the YD is related to a weak AMOC due to meltwater pulses in the North Atlantic, which forces a southward shift of the Intertropical Convergence Zone and its associated rainfall. Our records provide new evidence on the establishment of an "eastern forest corridor" in the nowadays semi-arid Caatinga allowing for past biotic interchanges of plant species.

1. Introduction

On millennial time scales, abrupt cooling events in the high latitudes of the North Atlantic were associated with decreases in the Atlantic meridional overturning circulation (AMOC) strength, such as Heinrich Stadial 1 (HS1, ~18-15 cal kyr BP) (McManus et al., 2004) and the Younger Dryas (YD, ~12.9–11.6 cal kyr BP) (Rasmussen and Thomsen, 2015). These oceanic changes have greatly influenced tropical ecosystems across both hemispheres particularly in South America, where the moisture is controlled primarily by rainfall fluctuations associated with the seasonal migration of the Intertropical Convergence Zone (ITCZ) that is due to changes in the low level atmospheric flow (Zhang and Delworth, 2005; González et al., 2008; Donohoe et al., 2013). Paleoclimate reconstructions and coupled climate models agree that the southward shift of the ITCZ and its associated tropical rainbelt promoted wetter conditions in the nowadays semi-arid northeastern (NE) Brazil during Heinrich stadials (HS) and YD (Arz et al., 1999; Behling et al., 2000; Haug et al., 2001; Wang et al., 2004; Zhang and Delworth, 2005; Leduc et al., 2007; Mulitza et al., 2017; Zhang et al., 2017), while drier conditions were recorded in northern South America (Peterson et al., 2000; Haug et al., 2001; González and Dupont, 2009). These climatic patterns would imply geographical shifts in biome boundaries in particular the Amazon rainforest-savanna boundaries, known to be very sensitive to climate change (Mayle et al., 2000). However, the long-term climate variability and its impact on the biodiversity in this area remain poorly understood. Speleothem $\delta^{18}O$ records from NE Brazil and Amazonia have revealed periodic swings from severely dry to wet conditions over the past 250 kyr during which, it was

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hypothesized that the region experienced periodic exchanges between the Amazon and Atlantic forests (Wang et al., 2004, 2017; Cruz et al., 2009). Cheng et al. (2013) have further suggested biotic exchanges during these intermittent wet periods along an eastern corridor connecting eastern Amazonia with northern Atlantic forest (Wang et al., 2004; Cheng et al., 2013) and a western corridor connecting western Amazonia with southern Atlantic forest (Cheng et al., 2013). Pollen records from the predicted eastern corridor in NE Brazil (De Oliveira et al., 1999; Behling et al., 2000; Dupont et al., 2010) indicate tropical rainforest expansion during the late Pleistocene-Holocene recurrent wet periods in an area that is currently dominated by semi-arid Caatinga vegetation. The well-resolved and -dated marine palynological (Dupont et al., 2010) and stable isotope records (Jennerjahn et al., 2004) from the continental margin off NE Brazil (offshore the eastern corridor) showed a succession of two major phases of vegetation response to enhanced precipitation during the cold HS1. These phases progressed from treeless vegetation largely composed of grass and shrubs to well-developed tropical rainforest vegetation during the latter part of HS1, suggesting a rapid response of regional vegetation to increased precipitation in the otherwise semi-arid region. Although these records provide significant insights into the vegetation development of NE Brazil, the link between millennial-time scale hydrological patterns and the long-term dynamics of biome boundaries, which in turn influence rainforest biodiversity, remain unclear. Moreover, changes in vegetation and its response to past rainfall variations during the YD cold reversal are poorly documented in this area. Here, we generated well-dated palynological and major elemental data from a marine sediment core collected from the continental margin offshore NE Brazil covering the YD. Our new records provide key insights into vegetation and hydrological changes on centennial resolution, suggesting a two-step pattern in the hydroclimate of the YD that has not been previously described from South American climate paleorecords. These climatic changes affected plant distribution and diversity in NE Brazil allowing recurrent expansions of tropical rainforest during the last deglaciation, in the nowadays semi-arid Caatinga. Thus, our records suggest the Caatinga as a potential corridor for considerable biotic interchange between the Amazon and Atlantic forests under past appropriate climate conditions, corroborating the hypothesized “eastern corridor” development between the eastern Amazonia and the northern Atlantic forests.

2. Modern climate, environmental setting and vegetation of northeastern Brazil

The northeastern region of Brazil is characterized by a semi-arid tropical climate (mean annual rainfall between 250 and 1000 mm; mean annual temperature between 24° and 26 °C) with a pronounced contrast between dry and wet seasons controlled mainly by the latitudinal position of the ITCZ and its associated tropical rainbelt. The wet season is mostly concentrated between March and May, (ITCZ at its southernmost position) while the long dry season occurs between June and February (ITCZ to the north of NE Brazil) (Hastenrath, 2006; Rao et al., 1996). The study area is located offshore of the Parnaíba River, which is the largest river system between the São Francisco and Amazon rivers. Presently, river discharge into the ocean is relatively low because of the semi-arid climate of NE Brazil. The continental shelf offshore the Parnaíba delta is approximately 50 km wide with a shelf break at 40 m water depth (Vital, 2014).

The vegetation of NE Brazil is primary Caatinga, a type of semi-arid vegetation, which consists of several physiognomic types ranging from open grassland with woody elements to xeric shrubland and thorn forest, to shrub woodland (Cole, 1986) (Fig. 1). Caatinga vegetation consists primarily of thorny and deciduous trees and scrubs, cacti, succulents, and drought-tolerant grasses (Kuhlmann, 1977). The most representative trees and scrubs belong to the Anacardiaceae (e.g. *Astronium*, *Schinopsis*), Apocynaceae (*Aspidosperma*), Bignoniaceae (e.g. *Tabebuia*), Euphorbiaceae (*Croton*, *Jatropha*), Malvaceae (e.g. *Cavanillesia*), and Fabaceae (e.g. *Ambulana*, *Caesalpinia, Calliandra, Senna, Mimosa*, *Pithecellobium*). Grasses, cacti, and herbs (e.g. *Aeschynomene*, *Borreria*, *Impomoea*, *Stylosanthes, Sida, Zornia*) are also common. In the less arid parts of the Caatinga, patches of deciduous forest, and evergreen gallery and flood plain forests occur along rivers, and are represented by *Geoffroea*, *Licania* and the palm *Copernicia*.

A few small islands of humid forests develop at altitudes over 500 m, or humid sierras, which are characterized by taller forests dominated by *Cedrella*, *Lecythis*, *Pithecellobium*, *Manilkara*, *Hymenaea*, *Inga*, *Lonchocarpus*, *Cordia*, *Machaerium*, *Pterocarpus*, *Dalbergia* and *Symphonia* (De Andrade-Lima, 1982). The Caatinga is bordered by Cerrado (savannah) to the west and Atlantic forest to the southeast, along the coastal stretch (Fig. 1a). In the northwest border, a narrow band of Cerrado separates Caatinga from the Amazon rainforest. The Brazilian Cerrado is a tropical savanna formation dominated mainly by *Byrsonima*, *Mimosa* and *Didymopanax*. The coastal vegetation, restricted to a small strip along the eastern coast, consists of Atlantic forest with high species diversity and endemism reflecting a humid climate with a short dry season (Nimer, 1989). Mangroves are also present in the coastal areas and along river estuaries (Cohen et al., 2012). The pollination systems of Neotropical forests are dominated by insects (entomophilous pollination), bats (chiropterophilous pollination), birds (ornithophilous pollination), and wind (anemophilous pollination). Entomophilous pollination is the most frequent pollination system of the Caatinga, Cerrado and evergreen tropical forests followed by ornithophilous and chiropterophilous pollination guilds, while anemophilous pollination is generally rare in tropical forests (Bawa, 1990; De Oliveira and Gibbs, 2000; Machado and Lopes, 2004).

3. Material and methods

We studied marine sediment core GeoB16205-4 (1°21.11′S, 43°05.80′W, ~1955 m water depth), retrieved off the Parnaíba River mouth (NE Brazil) in the western equatorial Atlantic Ocean during R/V *Maria S. Merian* cruise MSM20/3 (Mulitza et al., 2013). Core GeoB16205-4 is composed of weakly to moderately bioturbated, very dark grey to light brown foraminifer-bearing mud (Mulitza et al., 2013). Two thin turbidite layers at ~255 and 415 cm core depth have been described (Voigt et al., 2017). The age model for core GeoB16205-4 is based on 15 AMS ^{14}C measurements on monospecific samples of planktonic foraminifera *Globigerinoides sacculifer* (>150 μm) performed at the Poznan Radiocarbon Laboratory, Poland (please see all details regarding the age model in the supplementary materiel attached to this manuscript as well as Voigt et al. (2017)). The core is ~620 cm long and spans the interval between ~16.9 and 1.1 cal kyr BP. In this work, we investigated the section between ~265 and 10 cm corresponding to the time interval ~13–1.5 cal kyr BP.

3.1. Palynological analysis

Forty-seven sediment samples were taken at ~5 cm intervals allowing an average temporal resolution between ~65 and 100 years. Samples were prepared for palynological analysis using