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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

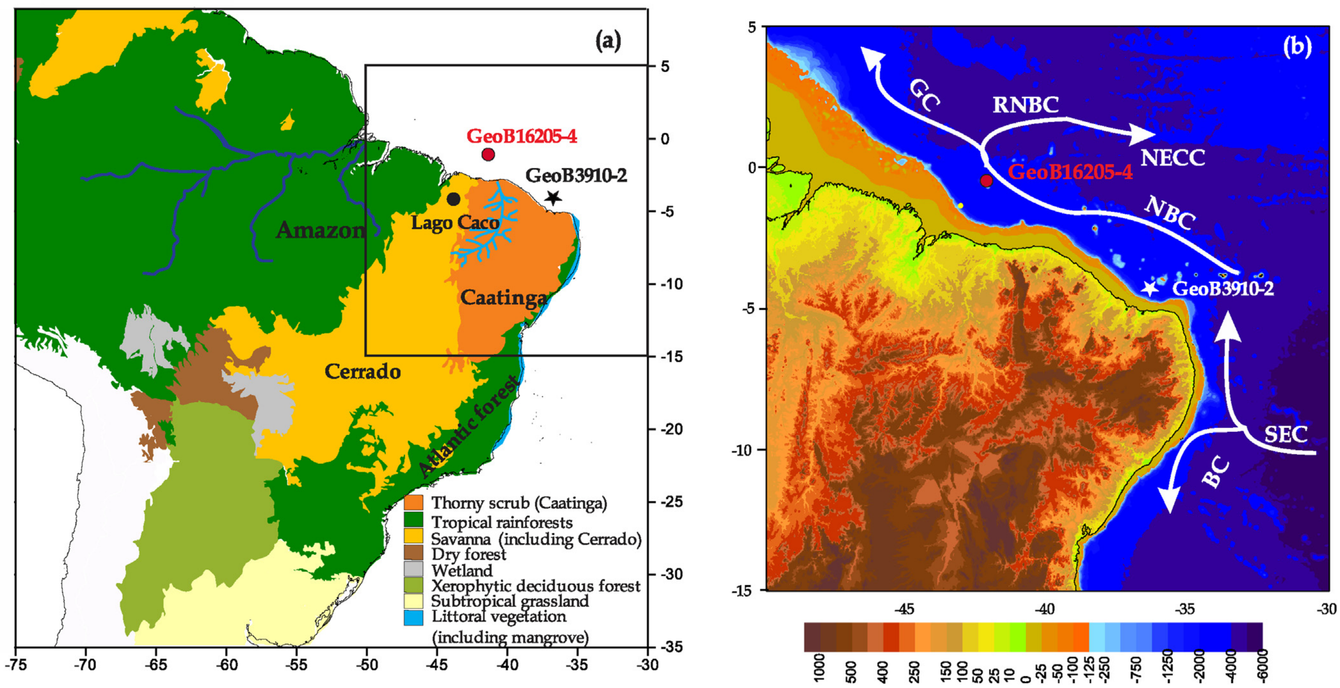

Fig. 1. (a) Map of major vegetation types in central and northern South America showing the location of marine sediment core GeoB16205-4. Indicated are the main stem and tributaries of the Amazon River (dark blue), the Parnaíba River (light blue), and the location of the Caatinga, Cerrado, Amazon and Atlantic forests. Marine sediment core GeoB3910-2 (Dupont et al., 2010) discussed in the text is also illustrated as well as the location of Lake Caço (Ledru et al., 2006). Rectangle delineates the zoomed area in map (b). (b) Topographic/bathymetric map of the study area showing the location of marine sediment core GeoB16205-4 and the nearby core GeoB3910-2 (Dupont et al., 2010) discussed in the text. Color scale in meters. The white arrows schematically indicate the flow direction of the Brazil Current (BC), Guiana Current (GC), North Brazil Current (NBC), retroflection of the North Brazil Current (RNBC), North Equatorial Counter Current (NECC), and South Equatorial Current (SEC). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

standard laboratory procedures (Faegri and Iversen, 1989). Sediment (2 cm^3) was decalcified with diluted HCl (10%), and treated with HF (40%) to remove silicates. One tablet of exotic *Lycopodium* spores (10,679 ± 426 spores/tablet) was added to the samples during the decalcification process in order to calculate palynomorph concentrations per ml (Bouimetarhan et al., 2009). After chemical treatment, samples were sieved over an 8 μm nylon mesh screen using an ultrasonic bath (maximum 60 s) to disaggregate organic matter. An aliquot (40–60 μl) was mounted on a permanent microscope slide. One to three slides per sample were counted at 400 and 1000 time magnification. Pollen grains were identified following Hooghiemstra (1984), Van Geel and Aptroot (2006) and the reference collection of the Department of Palynology and Climate Dynamics at the University of Göttingen (Germany).

We also counted organic-walled dinoflagellate cysts (dinocysts) following the online key for dinoflagellate cyst determinations (Zonneveld and Pospelova, 2015) as well as fresh water algae (*Botryococcus*, *Cosmarium*, *Pediastrum*, *Scenedesmus* and *Staurastrum*) and microscopic charred particles (<100 μm) on the same slides as those used for pollen.

The ratio of charred particles was calculated as the count of charred particles divided by the sum of charred particles, pollen and spore counts. To establish the reliability of our results, statistical errors (95% confidence intervals) of pollen percentages and concentrations were calculated following Maher (1972, 1981). The percentages errors depend solely upon the size of the sum and the proportion within the sum of the taxon of interest. Whereas the errors associated with pollen concentrations depend upon being able to assess and combine errors associated with measurement of sample volume, the quantity of exotic *Lycopodium* spores added, and the amount of exotic *Lycopodium* spores counted, as well as the size of the count of the taxon of interest.

3.2. X-ray fluorescence scanning

Elemental intensities of cores GeoB16205-4 were obtained by scanning the split core surfaces of the archive halves with an AVAATECH X-Ray Fluorescence (XRF) core-scanner at the MARUM, University of Bremen (Germany). The high-resolution XRF data were measured downcore in 2 mm steps. Here, we only used the intensities (counts/second) of Fe and Ca. We interpret variations in the Fe/Ca ratios as indicators of changes in terrigenous input to the ocean and thus as a proxy of continental hydroclimate (Zhang et al., 2015).

4. Results

The palynological content of the studied core was sufficient for appropriate analysis of most of the samples except for the upper 90 cm section that provided very low pollen counts and showed very low sedimentation rates. Therefore, the Holocene section that is poor in pollen and spores for proper analysis was excluded from the interpretation; we focus here on the interval ~13-10 cal kyr BP.

4.1. Fe/Ca variations and palynomorph concentrations

The Fe/Ca ratios recorded in sediment core GeoB16205-4, range from 0.4 to 7.6 (Fig. 2d). The Fe/Ca values increase between ~12.9 and 12.6 cal kyr BP and remain high until ~11.7 cal kyr BP. After that, Fe/Ca values decrease steadily until~11.2 cal kyr BP, when a marked decrease brings the record to minimum values at ~11 cal kyr BP. Sedimentation rates exhibit a salient increase during the YD with

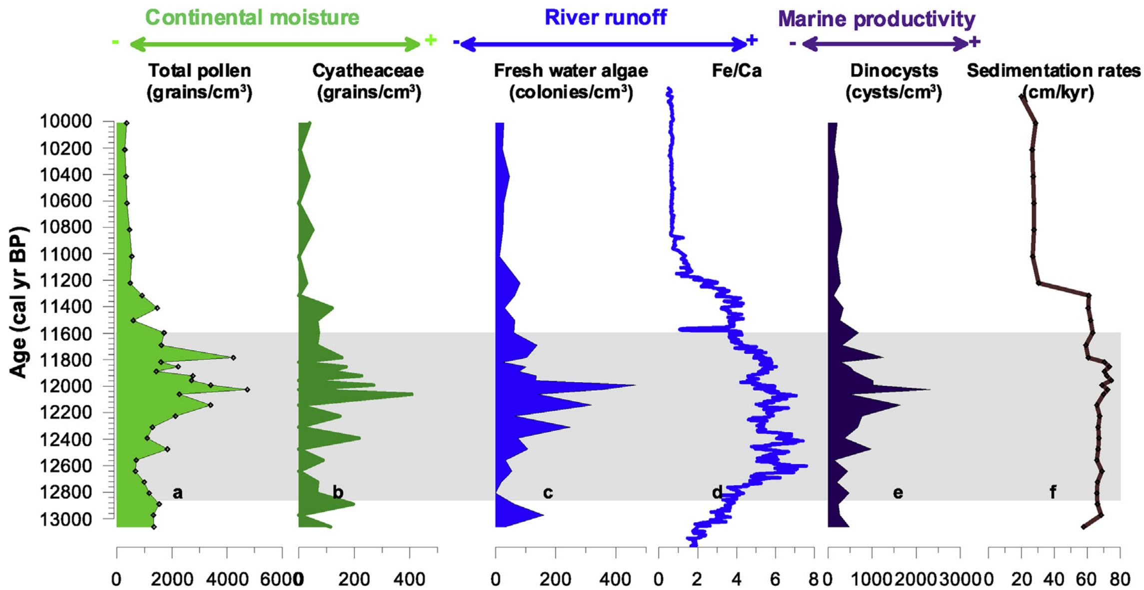

Fig. 2. Downcore variations of selected parameters in core GeoB16205-4. (a) Total pollen concentration; (b) concentration of non-degraded Cyatheaceae tree fern spores; (c) fresh water algae concentration; (d) Fe/Ca ratios; (e) dinocyst concentration; and (f) sedimentation rate (Voigt et al., 2017) based on the Bacon algorithm (Blaauw and Andres Christen, 2011). Horizontal grey shading indicates the time interval of the Younger Dryas (~12.9–11.6 cal kyr BP) (Rasmussen and Thomsen, 2015).

exceptionally high values of ~80 cm/kyr (Fig. 2f). Concentrations of terrestrial (pollen and spores) and marine (dinocysts) palynomorphs exhibit high values between ~12.9 and 11.6 cal kyr BP (peak at ~12 cal kyr BP), along with those of fresh water algae and Cyatheaceae fern spores (Fig. 2a–c, e).

4.2. Palynological reconstructions

The palynological record from sediment core GeoB16205-4 shows large changes in palynomorph concentrations and relative abundances as well as the dominance of the main taxa (Figs. 2 and 3). A total of 51 pollen and spore taxa were identified and the main taxa are listed in Table 1. Pollen assemblages are mainly dominated by Poaceae (grasses) reaching up to ~45%, Cyperaceae and *Rhizophora* with maximum relative abundances of ~42 and ~22%, respectively (Fig. 3). Arecaceae and *Didymopanax* pollen reach maximum percentages of ~14 and ~30%, respectively while Amaranthaceae reach ~12%. Between ~12.9 and 12.3 cal kyr BP, pollen percentages of Poaceae reach 30%, Amaranthaceae and *Borreria* reach 12% each, accompanied with the occurrence of Asteraceae, Anacardiaceae and *Artemisia* (Fig. 3). The interval between ~12.3 and 11.6 cal kyr BP shows a prominent increase in concentration values of total pollen and spores of tree ferns as well as organic dinocysts and fresh water algae (Fig. 2). Relative abundances of Cyperaceae pollen increase while pollen percentages of Amaranthaceae, *Borreria*, Asteraceae, Anacardiaceae and *Artemisia* decrease (Fig. 3). Pollen percentages of tropical rainforest taxa rise considerably with Arecaceae reaching up to ~13% and *Alchornea* ~9.5%, along with *Hedyosmum* ~7% and *Ilex* 4%. Percentages of *Rhizophora* increase to ~22%. Some of the main Cerrado taxa, represented by *Didymopanax* and *Mimosa* reach maximum percentages of ~30% and ~3% respectively.

After ~11.6 cal kyr BP, concentrations of pollen and spores decrease rapidly along with fresh water algae and dinocyst concentrations (Fig. 2). Grass pollen percentages start to increase around ~11.9 cal kyr BP to reach their highest values up to ~45% around ~10.4 cal kyr BP along with Amaranthaceae and *Artemisia* as well as elements from tropical rainforest (Arecaceae and Cyatheaceae). To avoid the bias of relative abundances being sensitive to changes of frequent individual taxa, rather than a vegetation signal, we plotted the concentrations of the main pollen taxa in the same Fig. 3 (horizontal bars) in order to accurately assess changes in pollen assemblages. Pollen concentrations are dominated by elements of tropical forest and Cyatheaceae spores, pollen of *Ilex*, *Hedyosmum* and aquatic taxa (*Typha*) as well as mangrove reaching up ~30 × 10^2 grains/cm^3. Concentrations of Cyperaceae pollen exhibit higher values of ~16 × 10^2 grains/cm^3. Pollen of the Caatinga and Poaceae represent only ~9.6 × 10^2 grains/cm^3 and ~10 × 10^2 grains/cm^3, respectively of the total pollen concentrations. Moreover, pollen concentrations show that most pollen taxa increase considerably during the YD except the semi-arid *Artemisia* and Asteraceae (Fig. 3). The palynological record shows a variety of pollen types during the interval between ~12.3 and 11.6 cal kyr BP, straddling the second phase of the YD. This interval, during which grass pollen concentrations and charred particle ratios display their lowest values, is characterized by higher tropical rainforest taxa concentrations as well as Cerrado and mangrove taxa (Fig. 3). In parallel, marine palynomorphs (dinocysts) record their highest concentrations during the second phase of the YD (Fig. 2e). Dinocyst concentrations show a striking increase of the dinocyst species *Trinovantedinium applanatum* and *Lingulodinium machaerophorum* (Fig. 3).

5. Discussion

5.1. Changes in regional vegetation and environmental conditions: the two phases of the Younger Dryas

The high pollen and spore contents, together with the increased Fe/Ca values and sedimentation rates of core GeoB16205-4 from ~12.9 until 11.6 cal kyr BP indicate increased terrestrial discharge to the western equatorial Atlantic during the YD (Fig. 2). Indeed, the large increase in the input of terrigenous sediments offshore NE Brazil was previously reported not only for the YD but also for HS1 based on geochemical and palynological data of marine cores from the region and interpreted as the consequence of increased fluvial input (Arz et al., 1999; Jennerjahn et al., 2004; Dupont et al., 2010; Zhang et al., 2015, 2017; Mulitza et al., 2017). More specifically,

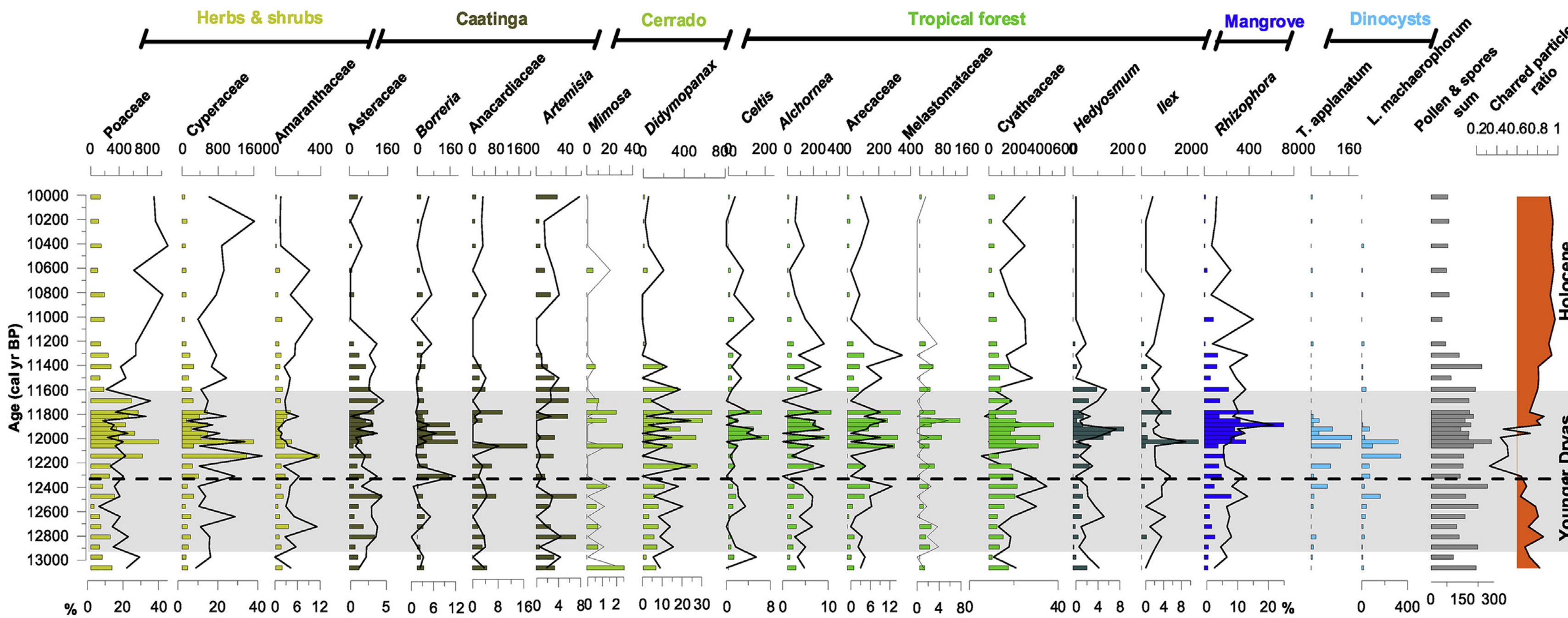

Fig. 3. Palynological data from marine sediment core GeoB16205-4 showing relative abundances (%) in the lower x-axis (lines) and concentrations (grains/cm^3) in the upper x-axis (horizontal bars) of the main pollen, concentrations of dinocyst species *Trinovantedinium applanatum* and *Lingulodinium machaerophorum* (cysts/cm^3), total pollen and spore counts on which pollen percentage calculations are based, as well as the ratio of charred particles. Horizontal shading indicates the Younger Dryas (~12.9–11.6 cal kyr BP (Rasmussen and Thomsen, 2015)) and the horizontal dashed line separates its two phases. Triangles indicate age control points.

Table 1
List of main pollen taxa identified in marine sediment core GeoB16205-4. Taxa are grouped according to their phytogeographical assignment based on De Oliveira et al. (1999) and Behling et al. (2000).

Pollen type	Family
Poaceae	
Cyperaceae	
Amaranthaceae (includesChenopodiaceae)	
Podocarpus	Podocarpaceae
Caatinga	
Artemisia	Asteraceae
Asteroideae	Asteraceae
Borreria (=Spermacoce)	Rubiaceae
Euphorbia	Euphorbiaceae
Anacardiaceae	Anacardiaceae
Fabaceae	Fabaceae
Bignoniaceae	Bignoniaceae
Malvaceae	Malvaceae
Stereospermum-type	Bignoniaceae
Cerrado (Tropical savanna)	
Acacia	Fabaceae-Mimosoideae
Mimosa-type	Fabaceae-Mimosoideae
Boscia	Capparaceae
Didymopanax	Araliaceae
Tropical rainforests	
Alchornea	Euphorbiaceae
Celtis	Cannabaceae
Arecaceae	Arecaceae
Piliostigma	Fabaceae-Faboideae
Melastomataceae	Melastomataceae
Hedyosmum	Chloranthaceae
Ilex	Aquifoliaceae
Littoral vegetation: Mangrove	
Rhizophora	Rhizophoraceae
Bog vegetation and swamp	
Typha	Typhaceae
Other elements	
Pinus	Pinaceae
Spores	
Cyatheaeceae	Cyatheaceae
Selaginella	Selaginellaceae

Zhang et al. (2015) suggested that the increased Fe/Ca ratios combined with high sedimentation rates in sediment cores off the Parnaíba River mouth indicate an enhanced supply of terrigenous material and interpreted it as increased river suspension input. Additionally, based on neodymium isotopes of bulk sediments, Zhang et al. (2015) ruled out the aeolian and Amazon fingerprints of sediments reaching the continental margin off NE Brazil and concluded that the delivery of terrestrial material to the study area occurred mainly via fluvial discharge, namely the discharge of the Parnaíba River drainage basin.

Atmospheric input is extremely low off NE Brazil since the prevailing winds blow from the Atlantic Ocean towards the continent (Garreaud et al., 2009; Govin et al., 2012) and the neodymium isotopic results from cores off the Parnaíba River mouth do not support a southeastward transport of Amazon suspension to the NE Brazilian continental margin (Zhang et al., 2015). A constant concern on palynological studies relates to the possible occurrence of species-selective degradation processes to post-depositionally alter the palynmorph association (e.g., Hopkins and McCarthy, 2002). At our study site, the sedimentation rates are 3–5 times higher than those of previously published sediment cores off NE Brazil (Arz et al., 1999; Jaeschke et al., 2007; Zhang et al., 2015). This results in low oxygen concentrations in pore waters and a quick burial of organic matter, sharply reducing the exposure time of palynomorphs to potentially oxygen-rich bottom waters. We thus, expect that the palynomorph associations at this site have not been significantly altered by degradation processes and can trustworthily be used to document changes in past climatic conditions. Therefore, the high pollen concentrations recorded in our data probably reflect both increased pollen production by the vegetation as well as enhanced transport of pollen by higher river activity associated with the changes of fluvial processes in the Parnaíba River drainage basin during such millennial-scale intervals. Taken together, our palynological reconstructions and XRF elemental data indicate enhanced precipitation over NE Brazil during the YD that promoted strong fluvial activity in the Parnaíba River drainage basin.

On millennial timescales, the enhanced rainfall over NE Brazil in response to Northern Hemisphere high-latitude cooling associated with periods of AMOC weakening was documented by stalagmite isotopic records (Wang et al., 2004; Cruz et al., 2009; Stríkis et al., 2015) and by marine palynological and sedimentological records (Arz et al., 1999; Behling et al., 2000; Dupont et al., 2010), as well as simulated with numerical climate models (Zhang and Delworth, 2005; Jaeschke et al., 2007; Mulitza et al., 2017). While the mentioned archives have provided clear evidence of humid environmental conditions as well as tropical rainforest expansion during times of a markedly weakened AMOC associated with North Atlantic cold stadials, most of them have either not covered the YD or have covered it only in low resolution (Hessler et al., 2010).

Our high resolution records indicate that the short YD event was not as uniform as previously thought and clearly reveal a succession of two major vegetation phases that progressed from a relatively open plant community with few patches of arboreal vegetation to a more diverse and dense woody vegetation (Figs. 3 and 4). During the first phase of the YD (~12.9–12.3 cal kyr BP), low pollen and spore concentrations along with low fresh water algae concentrations would suggest a relatively dry landscape (Figs. 2–4). Additionally, high charred particles ratios during this time interval may reflect enhanced fire activity probably caused by the expanded grass vegetation (Poaceae) observed before the YD (Dupont et al., 2010) which, would be in line with strong fires observed in Lake Caço at the end of the Pleistocene ~12.8 cal kry BP (Ledru et al., 2006). Moreover, a pronounced dry season would have been necessary to dry out the vegetation making it more susceptible to ignition (Osborne, 2008) which would corroborate the dry environment deduced by our results. In Lake Caço, this phase of early YD corresponds well with more open landscapes as indicated by increased *Cecropia* and Myrtaceae (Sifeddine et al., 2003). This period characterized by dry landscape and enhanced fire activity was followed by a sudden drop in Poaceae pollen and charred particles in our record, (Fig. 4a and b). Soon after ~12.3 cal kyr BP, the pollen record reveals that vegetation became denser as indicated by the high relative abundances, concentrations and diversity of the arboreal pollen (Figs. 3 and 4). During the second phase of the YD (~12.3–11.6 cal kyr BP), sedimentation rates are slightly higher than in the previous phase (Fig. 4g). Cyperaceae pollen is more prominent (Figs. 3 and 4) indicating the extension of wet areas along rivers and lakes. Moreover, increased pollen concentrations of *Alchornea*, *Celtis* and Arecaceae indicate the development of tropical rainforest suggesting much wetter conditions than during the previous YD phase (Figs. 3 and 4). Additionally, the increasing tree fern spore concentrations (Cyatheaceae) that would have grown in the more humid gallery forests provides another line of evidence to the precipitation increase during the second phase of the YD. Importantly, Caatinga is still present during the second phase of the YD (Figs. 3 and 4), indicating the coexistence of a variety of vegetation types that enriched the landscape of NE Brazil. In spite of its lower resolution and age model uncertainties, Lake Caço also shows a general trend towards more humid conditions during this second phase of YD, indicated by peaks in siderite and goethite fluxes (Sifeddine et al., 2003) and by the presence of elements typical of humid forests and gallery swampy environments such as

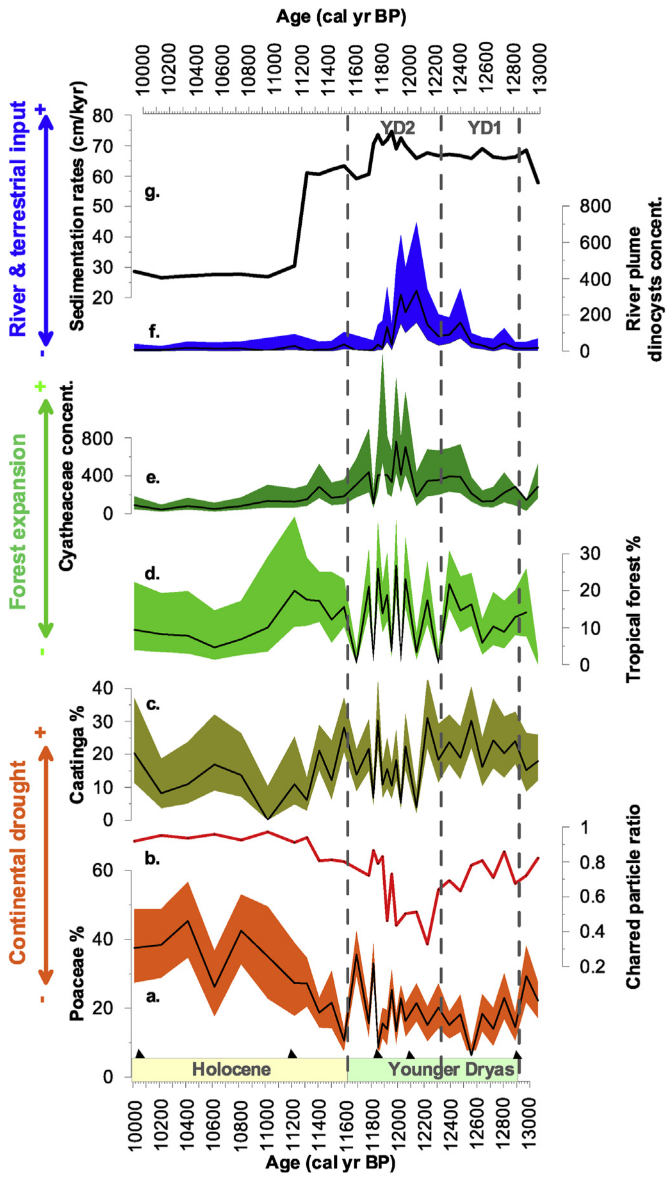

Fig. 4. Major palynological groups occurring in marine sediment core GeoB16205-4. (a): Grass-pollen percentages; (b): charred particle ratios; (c): pollen percentages of elements from the Caatinga (Anacardiaceae, *Borreria*, Asteraceae, Artemisia); (d): pollen percentages of elements from tropical forest (*Celtis*, *Alchornea*, Arecaceae, Melastomataceae); (e): concentrations (grains/cm^3) of Cyatheaceae tree fern spores from the tropical rainforest; (f): concentrations (cysts/ml) of the river plume dinocyst assemblage (*Trinovantedinium applanatum* and *Lingulodinium machaerophorum*); (g): sedimentation rates (Voigt et al., 2017). Percentages are based on the total pollen and spore sum shown in Fig. 3. Shadings indicate the 95% confidence interval calculated after Maher (1972, 1981). Dashed lines denote the two phases of the Younger Dryas (YD) as defined in this study. Triangles indicate age control points.

Moraceae-Urticaceae, Cyperaceae and Mauritia (Ledru et al., 2006).

In the marine realm, palynomorphs show increase in the concentrations of *Trinovantedinium applanatum* and *Lingulodinium machaerophorum* dinoflagellate cysts considered by Vink et al. (2000), in western equatorial Atlantic surface sediments, as a river plume assemblage occurring in stratified surface waters and reduced salinity environments rich in terrigenous nutrients (Fig. 4f). This suggests enhanced river runoff due to increased precipitation in the drainage basin of the Parnaíba River that supplied large amounts of terrigenous material and nutrients to the continental margin during the second phase of the YD. We therefore suggest moister continental conditions related to enhanced precipitation and high fluvial runoff compared to the previous YD phase. Increasing both freshwater supply and sediment load would also fit the observed development of mangrove forest (Fig. 3) and increased fresh water algae concentrations (Fig. 2c) as well as the lowered charred particle ratios (Fig. 4b). On the basis of a direct comparison between terrestrial palynomorphs and Fe/Ca values, we observe a slight decrease in Fe/Ca ratios during the second phase of YD which could be interpreted as a decline in rainfall. However, the decreasing Fe/Ca values can be attributed to the role of well-developed vegetation in controlling erosion, and therefore the input of terrestrial Fe diminishes during the second phase of YD, relative to the first phase. Fe/Ca values and sedimentation rates decrease dramatically after ~11.3 cal kyr BP together with concentrations of terrestrial palynomorphs and fresh water algae, while Poaceae pollen percentages and charred particles exhibit their highest values in the whole record.

These lines of evidence suggest a return to a more open and dry vegetation ~300 yr after the demise of the YD (Figs. 2–4). It is noteworthy that the delayed end of the YD in our record might result from age model uncertainties (Voigt et al., 2017).

5.2. *Impacts of the Younger Dryas in northeastern Brazil and their climatic implications*

We further compared our results with outputs from the transient TraCE-21k run, a coupled climate model simulation of the last termination including the YD using the Community Climate System Model CCSM3 (He, 2011; Liu et al., 2012; Shakun et al., 2012). The TraCE-21k was forced by changing orbital parameters, greenhouse gas concentrations, ice sheets, and meltwater fluxes based on geological reconstructions.

The shift from a moderately wet YD first phase to a much wetter second phase as reconstructed by our data is in agreement with annual rainfall variations in the Parnaíba River region as simulated by the TraCE-21k run, that shows a first pluvial phase from ~12.9 to 12.3 cal kyr BP and a second even stronger pluvial phase between ~12.3 and 11.6 cal kyr BP (Fig. 5). The second YD phase occurs simultaneously with increased pollen concentrations, high river plume dinocyst concentrations and high concentration of Cyatheaceae tree fern spores indicating more runoff and expanded tropical rainforest in NE Brazil (Dupont et al., 2010). Moreover, the model results are consistent with the concept of latitudinal displacement of the mean ITCZ position as the major driver of rainfall anomalies over the Parnaíba River region (Fig. 6). The southward migration of the ITCZ is triggered by changes in the interhemispheric surface temperature gradient (warming/cooling of the Southern/Northern Hemisphere tropics), which in turn is mainly driven by a decrease in the cross-equatorial oceanic heat transport associated with a weaker AMOC (Donohoe et al., 2013; Marshall et al., 2014; Mulitza et al., 2017).

In the TraCE-21k simulation, enhanced meltwater discharge from North American rivers (mainly St. Lawrence) leads to a reduction of the AMOC during the YD (Fig. 5) (He, 2011).

At the beginning of the YD second phase, the AMOC reaches its minimum strength associated with meltwater routing through the Mackenzie River (Carlson et al., 2007; He, 2011). Changes in the tropical interhemispheric surface temperature gradient are expected to evolve because of the reduced intensity of the AMOC such as the increase of the Southern Hemisphere temperature with respect to the Northern Hemisphere during the YD primarily during the second phase, as shown in Fig. 5b. The freshwater-induced reduction of the AMOC and its associated northward heat transport requires an adjustment of the interhemispheric energy balance through reorganization of the Hadley circulation, such that the ITCZ

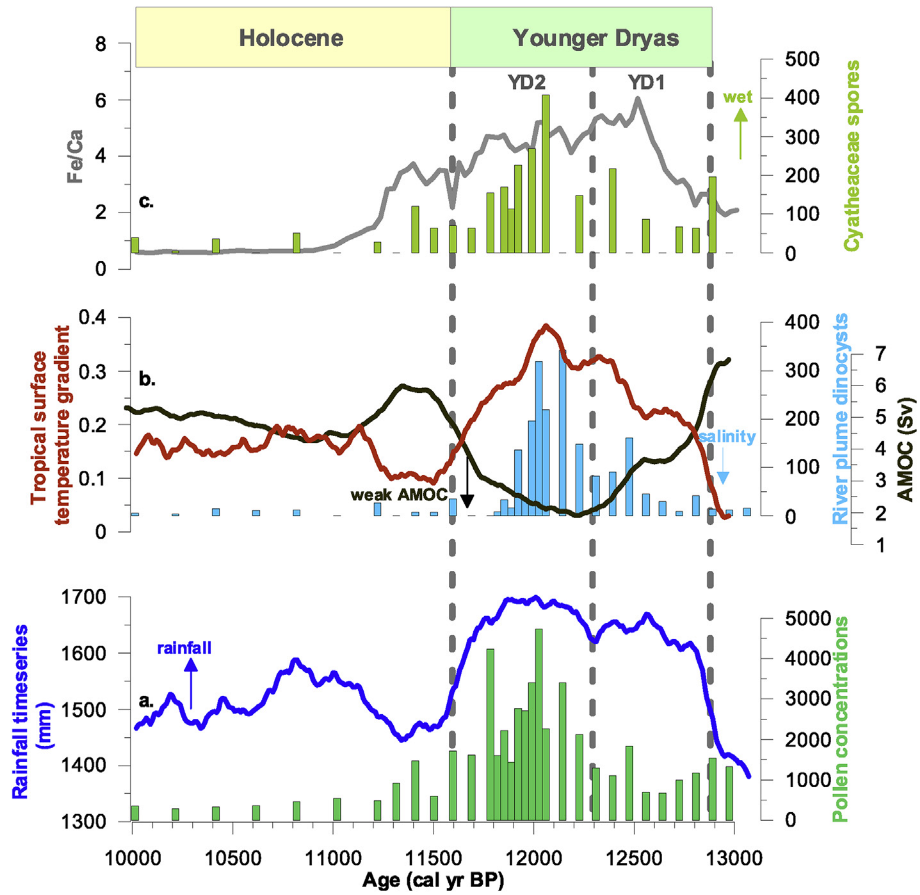

Fig. 5. Comparison of palynological records (this study) and TraCE-21k model output (Liu et al., 2012). (a): Total pollen concentrations (grains/cm^3) (dark green bars) and the modeled annual rainfall (mm) for the Parnaíba River region (47°W-41°W, 3°S-10°S) (blue curve). (b): Concentrations of the river plume dinocyst assemblage (cysts/cm^3) (*Trinovantedinium applanatum* and *Lingulodinium machaerophorum*) (blue bars), modeled tropical surface temperature gradient (in °C) (red curve) between the Southern Hemisphere (averaged over 20°S-0°) and the Northern Hemisphere (averaged over 0°-20°N) from the TraCE-21k transient simulation (red curve), the strength of the AMOC (black curve) measured as the overturning stream function maximum at the equator (in Sv). (c): Cyatheaceae fern spores concentrations (grains/cm^3) (light green bars) and Fe/Ca ratios. All model time series were smoothed with a 100-yr boxcar filter (moving average). Dashed lines denote the two phases of the Younger Dryas (YD) as defined in this study. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

undergoes a southward latitudinal displacement consistent with the relative warming of the Southern Hemisphere (Cvijanovic and Chiang, 2013; Kageyama et al., 2013; Marshall et al., 2014; Talento and Barreiro, 2015). As a result, the mean ITCZ reaches its southernmost position during the second phase of the YD, which led to increasing rainfall over NE Brazil and the Parnaíba River catchment (Fig. 6).

By these means, the numerical modeling experiment and palynological reconstructions reveal a predominantly wet climate during the YD in today's semi-arid NE Brazil, with higher humidity during its second phase, namely between ~12.3 and 11.6 cal kyr BP, due to a southward displacement of the ITCZ and its tropical rainbelt, a result that was not previously documented in the region.

5.3. Intermittent opening of forest corridors during the last deglaciation: "eastern corridor" activation and its biogeographical implications

The comparison of our palynological and geochemical records from marine core GeoB16205-4 with the TraCE-21k results indicate wet conditions at the Parnaíba River drainage basin over NE Brazil during the YD implying (Fig. 5): (i) the fast response of the vegetation to the increased precipitation starting ~12.9 kyr BP; and (ii) an even stronger second pluvial phase within the YD between ~12.3 and 11.6 cal kyr BP. Additionally, Zhang et al. (2015) suggest, based on geochemical and isotope studies, much higher precipitation and fluvial discharge during HS1 and the YD off the Parnaíba River. These paleoenvironmental changes are similar to those described by Dupont et al. (2010) based on an HS1 pollen record located further southeast offshore NE Brazil (core GeoB3910-2, Fig. 1). Dupont et al. (2010) describe a shift from dry to substantially wet conditions during HS1, with a much wetter phase during the second HS1 phase between ~16.5 and 15 cal kyr BP. We thus infer that tropical rainforest expansion occurred in the currently semi-arid NE Brazil during these intermittent wet intervals indicating the recurrent occurrence of wetter climate over NE Brazil during the last deglaciation. A similar pattern of significant increase in moisture availability has been reported around ~17.3 cal kyr BP from continental archives such as Lake Caçó (NE Brazil), where a clear transition from steppe to dense rainforest occurred around ~15.5 cal kyr BP during periods of weak AMOC as demonstrated by palynological data and hydrogen isotope records (Ledru et al., 2006; Jacob et al., 2007). Additionally, speleothem $\delta^{18}O$/travertine records from the easternmost Amazon/interior of NE Brazil reveal recurrent wetter conditions during Pleistocene stadials (Wang et al., 2004, 2017). Taken together, our results show that the episodic periods during which NE Brazil and particularly the Parnaíba River basin received high amounts of rainfall, have influenced

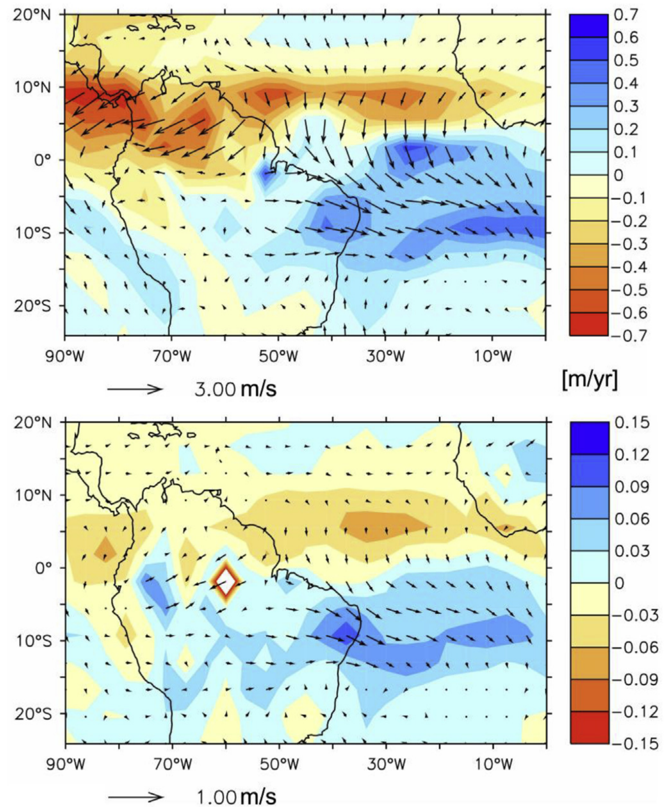

Fig. 6. Maps of mean precipitation and surface wind anomalies for the core of the first (12.7–12.3 kyr BP) and second (12.2–11.8 kyr BP) Younger Dryas (YD) phases as simulated by the TraCE-21k (Liu et al., 2012). Upper panel: Difference between the first YD phase and the pre-YD interval 13.5–13.0 kyr BP. A meridional dipole of anomalous precipitation along with northerly surface wind anomalies in the tropics indicates a southward shift of the Intertropical Convergence Zone (ITCZ). Lower panel: Difference between the second YD phase and the first YD phase, showing a further displacement of the ITCZ towards the South.

the plant distribution of the region. The paleoclimate patterns described above imply the development of dense forests that could have replaced or mixed with the Caatinga over NE Brazil, fostering the extraordinary diversity of neotropical forests. One could argue that the increase in arboreal pollen in our record could be due to highly dynamic patchy vegetation namely during the second phase of YD between ~12.3 and 11.6 cal kyr BP instead of the existence of forest corridors. A high frequency of vegetation unit displacements during the second phase of YD would refute full changes in the limits of vegetation biomes and the existence of forest corridors suggested here. However, the results presented here for the second phase of YD compare well with the vegetation development during HS1 (Dupont et al., 2010), where a shift from a dry to a much wetter phase is described for the second phase of HS1 between ~16.5 and 15 cal kyr BP. Additionally, this pattern is similar to the transition from steppe to dense rainforest recorded around ~15.5 cal kyr BP at the Lake Caçó (NE Brazil) based on palynological data and hydrogen isotope records (Ledru et al., 2006; Jacob et al., 2007). Therefore, our analysis of the YD, which complements the above-mentioned studies, indicates that the deglacial climate in NE Brazil swung drastically between dry and wet conditions in contrast to the much more stable conditions in western Amazonia (Wang et al., 2017). Moreover, this record corroborates other pollen records that indicate late Pleistocene forest expansion in a region currently dominated by semi-arid Caatinga vegetation (Behling et al., 2000; De Oliveira and Gibbs, 2000). The broad similarities in the climate evolution recorded at different sites in NE Brazil (e.g., Arz et al., 1999; Behling et al., 2000; Jennerjahn et al., 2004; Dupont et al., 2010; Zhang et al., 2015; Mulitza et al., 2017; Zhang et al., 2017) including speleothem hydrological records (Wang et al., 2004; Stríkis et al., 2015) support the key paleoclimate pattern of humid conditions during the second phase of YD implying the development of dense forests. The climatic reconfigurations across time and space have allowed the establishment of potential forest corridors during certain intervals promoting the exchange of species between biomes that today appear as separate entities (e.g. Wang et al., 2004; Werneck et al., 2011; Cheng et al., 2013). This interpretation is consistent with the hypothesized eastern corridor development, using speleothem isotope records, between the eastern Amazonia and the northern Atlantic forest (Cheng et al., 2013).

Some studies based on the phylogenetic analysis of e.g. lizards (Prates et al., 2016) and plants (Santos et al., 2007) have inferred connections between the Amazon and Atlantic forest during the Pleistocene. Furthermore, distribution patterns of South American birds agree with the existence of an eastern corridor (Ridgely and Tudor, 1994; Ridgely et al., 2007). In the same direction, modeling studies addressing the stability of biogeographical units in NE Brazil, also found that the Atlantic forest expanded during the LGM, offering more suitable conditions for exchange with Amazonian biomes (Leite et al., 2015). Our palynological reconstruction from marine core GeoB16205-4 emphasizes the considerable effect of the moisture availability during the YD on the vegetation changes of NE Brazil, which would have influenced geographical shifts in tropical rainforest boundaries allowing past biotic interchanges between Amazonia and the Atlantic forest predicted by Cheng et al. (2013) that would provide a new concept for understanding biodiversity in tropical Brazil. Our records not only corroborate the existence of a connection between the Amazon and Atlantic forests but also posts a new biogeographic scenario that privilege the opening of a forest corridor in the hypothesized "eastern corridor" challenging the idea that the high diversity and endemism of Caatinga is the result of long-term climatic stability (Dynesius and Jansson, 2000; Wiens and Donoghue, 2004; Jablonski et al., 2006).

6. Conclusions

Our combined palynological and geochemical records off the Parnaíba River mouth provide new information on the deglacial vegetation history and hydrologic variability in NE Brazil. The short YD event, a period of higher precipitation in the studied area displayed two different phases. A first relatively wet phase (~12.9–12.3 cal kyr BP) was characterized by heterogeneous vegetation types including grasses, Atlantic forest, gallery forest and the Caatinga dry forest. A second much wetter phase (~12.3–11.6 cal kyr BP) was characterized by the expansion of tropical rainforest inland and the occurrence of river plume dinocyst assemblages in front of the Parnaíba River mouth. The results indicate that the highest amount of rainfall over the Parnaíba River basin, during the second phase of the YD conjoined largely with the latitudinal displacement of the ITCZ associated with a reduced AMOC. The proposed two-phase vegetation sequence during the YD, which has not been previously documented in South America, provide another line of evidence on the establishment of a forest corridor, in the nowadays semi-arid region, that might have provided new paths of dispersal between currently separated rain forest biomes of NE South America; the Amazon and the Atlantic forest during intermittent wet intervals of the last deglaciation over NE Brazil. Our palynological record has great ecological significance as much as it deals with one of the biggest dry forests in the world offering an important complement to recently published biogeographical records from the region.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.quascirev.2018.05.026.

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