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6000 years of monsoon-driven east–west antiphasing of northeastern Brazil vegetation

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ABSTRACT

Northeastern Brazil (NEB) is characterized by irregular rainfall distribution and various vegetation types, such as the xerophilous Caatinga in the east, Cerrado and Amazon rainforests in the west. Sediment cores and speleothems show that the region was subjected to strong climatic changes during the Holocene. To reconstruct related vegetation responses and biomass burning, we present a synthetic review based on nine pollen published records covering the last 6000 years. Our regional environmental reconstructions reveal four intervals of changes, influenced by the position and intensity of an east-west moisture band across NEB, in phase with South America Summer Monsoon variability. Between 6.0 and 5.2 ka BP and 5.2–4.2 ka BP, changes in the distribution of the dry forest Caatinga, Cerrado and Amazon Forest were driven by oscillating precipitation in a general pattern dry western/moist eastern NEB. Similar changes amongst sites were correlated to their location either within or outside the moisture band. Between 4.2 and 2.6 ka BP, Caatinga expanded in the eastern NEB, while Cerrado and Amazon forests became established in western NEB. This vegetation shift matches the moist western/dry eastern NEB climate around 4.2 ka BP, consistent with TraCE-21k simulations and speleothem records. From 2.6 ka BP onwards, biomass burning observed under dry or wet conditions was related to a marked increase in anthropogenic activities. For the last 6000 years NEB's vegetation boundaries have been in phase with the summer insolation, the oscillations of the South America Summer Monsoon, and the positions of the convergence zones which delimited a band of moisture throughout specific location of NEB. Human activities were not found to be directly affected by the humidity gradient; instead, humans have relied on each biome's resources. Investigating the extent of climatic and human influences on NEB vegetation in the past is crucial to discussing the effectiveness of current conservation policies in the region.

1. Introduction

Northeastern Brazil (NEB) is a very populated region comprising an area of 1558 million km^2 and 54.6 million people, accounting for 26.9 % of Brazil's total population (IBGE, 2022a). It is the region with Brazil's highest poverty rate, where 80 % of agricultural labor is composed of smallholding, subsistence farming (IBGE, 2022b). Owing to its considerable size and particular orography, the region has diverse patterns of climate and vegetation. NEB exhibits a warm tropical climate to the east and west and a semi-arid climate in the eastern central region (Alvares et al., 2013). This basic pattern essentially controls the distribution of four out of six Brazilian biomes, from east to west: Atlantic Forest, Caatinga, Cerrado, and Amazon Forest (IBGE, 2021), all of which have high levels of endemism and plant relics (Moro et al., 2016; Oliveira et al., 2004; Vieira et al., 2019). Current distribution in species richness is a result of ecological and evolutionary processes besides past climate changes. For example, niche models (Ledo and Colli, 2017; Sobral-Souza et al., 2015) and recent pollen-based studies (Bouimetarhan et al., 2018; Ledru and de Araújo, 2023) have pointed out that during the Quaternary the region hosted biotic routes that connected the Amazon and Atlantic Forests by ecological migration corridors through the NEB Cerrado.

Identified as one of the most distinctive and important biodiversity

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centers in Brazil and the whole of South America (Moro et al., 2016; Oliveira et al., 2004; Vieira et al., 2019), NEB is a region of particular interest for studying vegetation dynamics, notably in the context of climatic changes. Phytosociological surveys have provided direct evidence of specific floristic composition and biodiversity in NEB plant communities, distinguishing the Cerrado (e.g. Calixto-Júnior et al., 2021; Saraiva et al., 2020), the Caatinga (e.g. Macêdo et al., 2024; Moro et al., 2014; Souza et al., 2022), the Atlantic Forest (Lôbo et al., 2011; Oliveira et al., 2004), and the Amazon Forest (Araujo and Pinheiro, 2012). However, these surveys are limited to one or two decades, and thus they lack observational data of biodiversity responses to long-term climatic changes; it is this which makes paleoecological archives a unique tool which can fill the observation gaps needed to investigate vegetation changes beyond the relatively short instrumental period (Chevalier et al., 2020).

The Mid-Holocene (MH, 8500 to ~4200 cal yr BP) is defined by a maximum of insolation in the precession cycle, and interhemispheric thermal variability of the Atlantic Ocean surface which strongly impacted the climate of NEB (Custódio et al., 2024; Gorenstein et al., 2022; Prado et al., 2013). Speleothem-based reconstructions showed a dipole between northern and southern Brazil (Bernal et al., 2016; Wang et al., 2017) and an east–west moisture gradient across NEB during the MH (Cruz et al., 2009; Utida et al., 2020). However, the responses of the vegetation, and more particularly the changes in the distribution of the Cerrado and Caatinga, are still poorly described in the literature. In Central and Southeastern Brazil, MH multiproxy compilations, predominantly pollen and charcoal, showed that regional vegetation responses (e.g. Ledru et al., 1998; Smith and Mayle, 2018) and demographic shifts were linked to large-scale climate changes (Flantua et al., 2016; Prado et al., 2013; Riris and Arroyo-Kalin, 2019).

In NEB, anthropogenic activities are observed since the Late Pleistocene (Goldberg et al., 2016; Lahaye et al., 2015; Martin, 2013; Souza et al., 2020). Archeological sites include two global geoparks, Seridó and Araripe (Global Geoparks Network, 2024), and one world heritage site, the Serra da Capivara National Park (UNESCO, 2024), which presents a rich collection of lithic artifacts, bonfire remains, rock paintings, and human skeletal remains (Bueno and Isnardis, 2018; Guidon et al., 1994; Martin, 2013). During the Early and MH, hunter-gatherer groups inhabited rock shelters and open fields (Martin, 2013; Melo, 2007), while the Late Holocene (LH) was dominated by agriculture and pottery-making communities based near the coastline (Davis and Navarro, 2023; Santos et al., 2012), water courses, interfluves, and highlands (Martin, 2013; Souza et al., 2020). These groups were related to the Jê and Tupi-Guarani cultures that inhabited the Amazon Forest, the Caatinga, the Cerrado, and Atlantic Forest in NEB (Dantas et al., 1992; Souza et al., 2020), with land use practices based on crop cultivation, reduced use of fire, and no significant deforestation to speak of (Sluyter and Duvall, 2016). However, these practices changed post-1492 CE (Koch et al., 2019) upon the arrival of Europeans in NEB. From 1500 CE onwards, human land use shifted to intense deforestation and the predominant use of fire, livestock, pastures, and extensive agriculture (Moura et al., 2019; Prado Jr, 2011; Sluyter and Duvall, 2016). Today, in NEB only 11 % of Caatinga natural cover and 19.8 % of Cerrado remains on account of human disturbance (Araujo et al., 2023; Vieira et al., 2021), while 24 % of the Amazon Forest and 13 % of the Atlantic Forest remnants are extremely fragmented due to agricultural expansion, illegal logging, and cattle ranching (Lins-e-Silva et al., 2021; Silva-Junior et al., 2022).

To address the issue of the responses of the northeastern biomes to climate changes during the last 6000 years, we here present a synthetic review of NEB pollen and charcoal records. Results were discussed at a regional scale and included within the paleoclimatic framework described by previous speleothem studies (Cruz et al., 2009; Stríkis et al., 2011; Utida et al., 2020, 2023) and a single pollen study (Hermanowski et al., 2012); we aimed to differentiate the responses of climate and human activities. We first introduce the environmental attributes, the criteria for selecting pollen records, and the methods employed to evaluate the vegetation changes within the regional paleoclimatic framework. We follow this by trying to correlate the impact of human activities on vegetation changes within our regional reconstruction. Finally, we conjecture about our results' implications for NEB's biodiversity and conservation and summarize the main conclusions.

2. Study area

2.1. Climate

In western NEB, the rainy season occurs during the period October–March (5–6 months), and is modulated by the South America Monsoon System (SAMS; Vera et al., 2006), reflecting the annual insolation cycle sustaining a land–sea thermal contrast and inland low-level moisture flux from the tropical North Atlantic Ocean (Fig. 1a) (Nascimento, 2014). The SAMS southern boundary between 10° and 15°S can also feed rainfall into southwestern NEB (Fig. 1a) depending on sea surface temperatures in the South Atlantic (Nascimento, 2014) and the position of the South Atlantic Convergence Zone (SACZ), a distinctive feature of the SAMS (Kodama, 1992). The dry season in western NEB starts in May with the SAMS weakening and the northward shift of the Intertropical Convergence Zone (ITCZ, Vera et al., 2006), a line of clouds formed by the convergence of the northeast and southeast trade winds near the geographic Equator. The ITCZ interannual shifts are influenced by the semiannual insolation cycles and thermal variability between North/South tropical Atlantic Ocean, causing precipitation seasonality over NEB (Marengo et al., 2022). However, precipitation still occurs on the northwestern coast until July (Nascimento, 2014), modulated by squall lines and easterly wave disturbances (Barros and Oyama, 2010).

In eastern NEB, the rainy season occurs and peaks during February–May (4–5 months), induced by the seasonal southward migration of the ITCZ (Fig. 1a) (Marengo et al., 2017) during the negative phase of the South Atlantic Subtropical Dipole (SASD, Wainer et al., 2021). However, most of the eastern and central NEB receive only 300–800 mm of annual precipitation (Marengo et al., 2020) due to the influence of the anticyclonic circulation of the South Atlantic Subtropical High (Gorenstein et al., 2023). The start of the dry season in eastern NEB occurs from March to May and lasts around 7–8 months, with the seasonal northward migration of the ITCZ during a positive phase of the SASD (Marengo and Bernasconi, 2015; Vera et al., 2006; Wainer et al., 2021). On the eastern coast of NEB, the rainy season continues until June, modulated by easterly wave disturbances and sea breeze circulations carrying humidity from the tropical Atlantic (Nimer, 1989).

From east to west, the regional mean annual precipitation ranges between 400 and 1800 mm (Fig. 1a) (INMET, 2023; Silva and Kousky, 2012), while the regional mean annual temperature varies between 23° and 28 °C (Fig. 1b), with a mean minimum that never falls below 20 °C and a mean maximum that does not exceed 32 °C (INMET, 2023). Both precipitation and temperature exhibit significant variability across the region, as the seasonal displacement of the ITCZ combined with the monsoon convection produces an east–west gradient of mean temperature and length of the rainy season. Ombrothermic diagrams of the historical mean month rainfall from the last 30 years (Figs. 1c and 1991–2020) show that from east to west the cities of Natal, Fortaleza, Teresina, São Luís, and Carolina have a total annual precipitation variability superior to 500 mm; from north to south the cities of Barbalha and Bom Jesus da Lapa show that this variability exceeds 800 mm (Fig. 1c). The total mean annual temperature varies +1 °C from east to west and +1.5 °C from north to south (Fig. 1c).

At interannual to lower frequency timescales, regional rainfall anomalies are mainly modulated by sea surface temperature (SST) anomalies in the Atlantic and Pacific Oceans (Marengo et al., 2017). Between February and May, a relatively warmer (colder) tropical South

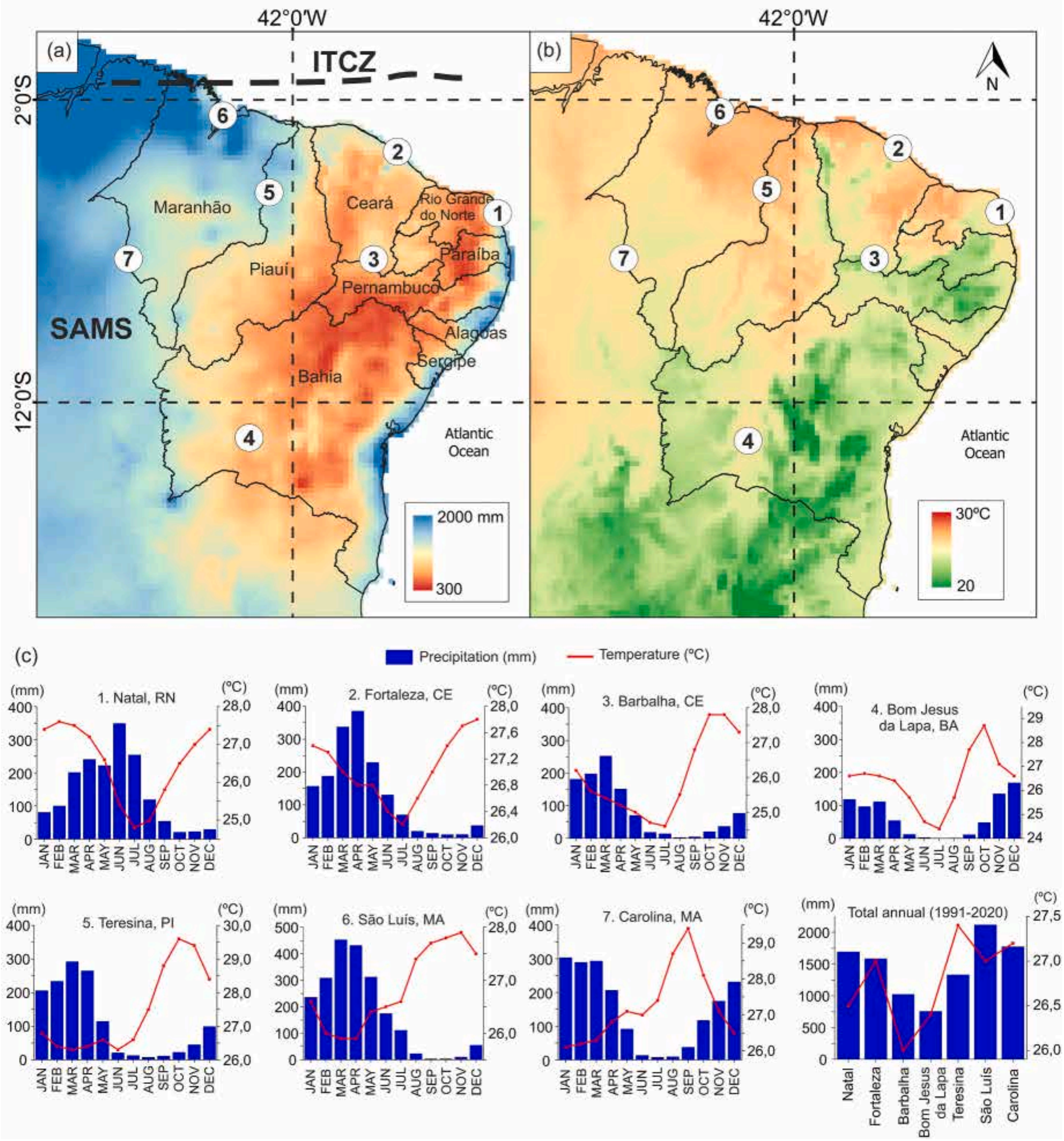

Fig. 1. Map of NEB showing a) mean annual precipitation (1991–2020) and b) annual mean temperature (1991–2020) (source: Fick and Hijmans, 2017). The ITCZ (dashed line) associated with the SAMS during the austral summer (December, January, and February), the apex of the SAMS. c) Ombrothermic diagrams of historical mean month rainfall (blue bars) and mean monthly temperature (red line) from the last 30 years (1991–2020) from cities located across east–west/north–south transect: 1. Natal (Rio Grande do Norte), 2. Fortaleza (Ceará), 3. Barbalha (Ceará), 4. Bom Jesus da Lapa (Bahia), 5. Teresina (Piauí), 6. São Luís (Maranhão), 7. Carolina (Maranhão) (source: INMET, 2023). Black lines represent the territorial limits of the region's nine states.

Atlantic tends to favor a southward ITCZ bias and above (below) normal precipitation over NEB (Marengo et al., 2017). The region is therefore subject to recurrent drought episodes that can be intensified by the occurrence of El Niño in the tropical Pacific Ocean and during the positive phase of the SASD that displaces the ITCZ northward due to SST anomalies of the tropical and South Atlantic (Gorenstein et al., 2023; Marengo et al., 2020; Sobral Verona et al., 2023).

2.2. Amazon Forest

Located in the northwestern lowlands of Maranhão state (Fig. 2), the Amazon rainforest covers 112,500 km^2 (7 % of the NEB area) (IBGE, 2021). The rainy season lasts from January to July (7 months), the mean annual temperature ranges from 25° to 27 °C, and mean annual precipitation is higher than 1800 mm (INMET, 2023). The rainfall is modulated by the ITCZ between January and May (Nascimento, 2014), and by squall lines and easterly wave disturbances from May to July (Barros and Oyama, 2010). The seven-month long rainy season with constant humidity enables the establishment of evergreen rainforest, composed of riparian forests, dense ombrophilous, and open ombrophilous forests in flooded and unflooded plains with the presence of palm trees (Araujo and Pinheiro, 2012). In flooded plains, floating islands are characterized by vegetation rooted on the thick organic matter layer instead of firm soil (Araujo and Pinheiro, 2012). The species with the highest value are *Euterpe oleracea* (Arecaceae) (42.75 %), *Virola surinamensis* (Myristicaceae) (18.12 %), *Mauritia flexuosa* (Arecaceae) (13.27 %), *Cecropia pachystachia* (Urticaceae) (8.57 %), *Montrichardia arborescens* (Araceae) (3.49 %), *Philodendron* sp. (Araceae) (2.39 %), and

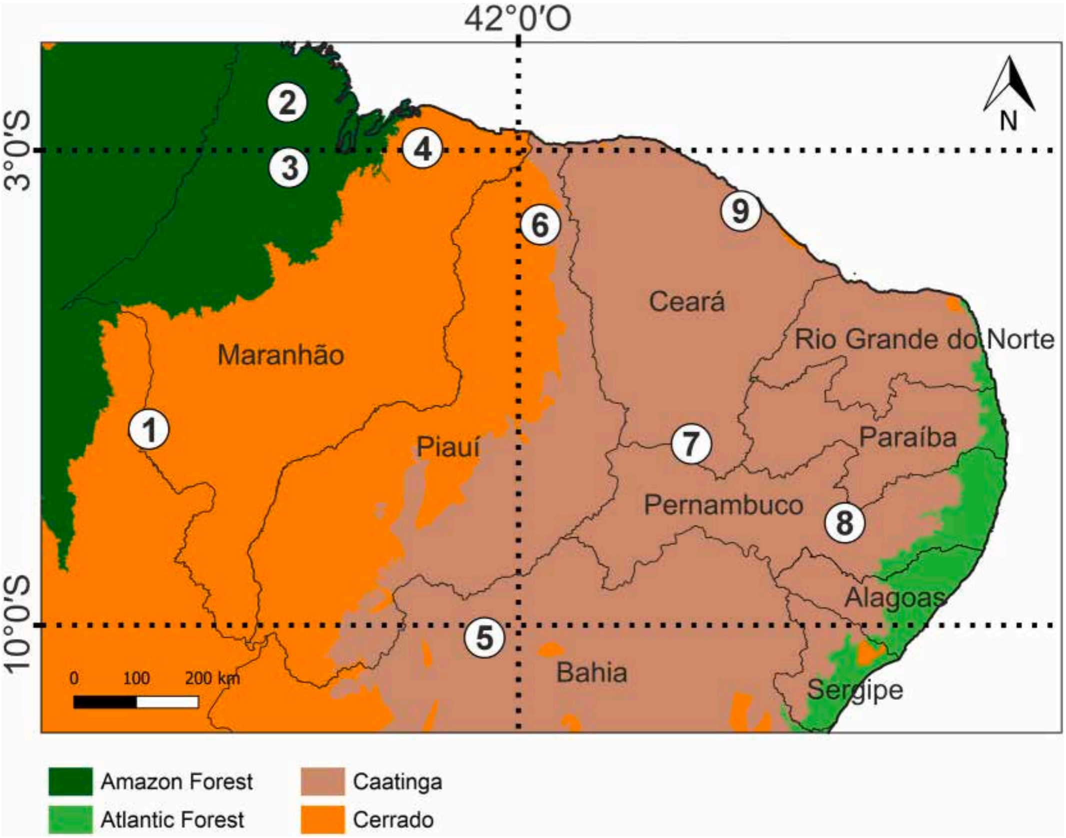

Fig. 2. Map of NEB showing state boundaries, the distribution of the biomes, the location of the pollen records (white circles) discussed in this study: 1. Chapada das Mesas (Xavier et al., 2024), 2. Cabeludo (Moraes et al., 2022), 3. Lake Formoso (Moraes et al., 2021), 4. Lake Caço (Ledru et al., 2006), 5. Icatu Valley (Oliveira et al., 1999), 6. Sete Cidades (Xavier et al., 2022), 7. Araripe Forest (Guerra et al., 2024), 8. Catimbau (Moraes et al., 2020), 9. Serra do Maranguape (Montade et al., 2014).

Tapirira guianensis (Anacardiaceae) (1.97 %) (Araujo and Pinheiro, 2012). In the non-floating islands, vegetation is well rooted in the firm soil layer, and is characterized by *Montrichardia arborescens* (Araceae) (32.28 %), *Virola surinamensis* (Myristicaceae) (2.49 %), and *Philodendron* sp. (Araceae) (2.41 %) (Araujo and Pinheiro, 2012). In the open flooded plains where vegetation is predominantly herbaceous, the most common taxa are *Piper* sp. (Piperaceae), *Neptunia oleracea* (Fabaceae--Mimosoideae), *Paratheria prostrata* (Poaceae), *Marsilea deflexa* (Marsileaceae), and *Heliotropium lanceolatum* (Boraginaceae) (Braga, 2006). Pollen assemblages from Amazon lowland forests are composed of Moraceae/Urticaceae, *Alchornea* (Euphorbiaceae), *Cecropia* (Moraceae), *Celtis* (Cannabaceae), *Hyeronima* (Phyllanthaceae), *Ilex* (Aquifoliaceae), *Podocarpus* (Podocarpaceae), and *Bursera* (Burseraceae) (Colinvaux et al., 1999; Gosling et al., 2009).

2.3. Atlantic Forest

The Atlantic forest stretches over 164,700 km^2 (10 % of the NEB area) (Correia Filho et al., 2019) along the eastern coast from sea level to low-altitude plateaus, <500 m above sea level (asl) (Fig. 2) in the states of Alagoas, Sergipe, Pernambuco, Paraíba, and Rio Grande do Norte, occurring also at a number of isolated mountains and plateaus of Bahia and Ceará (Lôbo et al., 2011; Silva and Casteleti, 2005). The rainy season lasts from January to August (8 months), with annual rainfall between 1500 and 2000 mm, and temperatures ranging from 20° to 27 °C (INMET, 2023). Precipitation is modulated by easterly wave disturbances and sea breeze circulations carrying humidity from the tropical Atlantic and cold fronts along the coast (Correia Filho et al., 2019; Nimer, 1989), creating orographic rainfall and frequent fogs; this abundant moisture maintains the rainforest which is composed of evergreen, dense ombrophilous and open ombrophilous forests, and semi-deciduous forests with shade-tolerant and light-demanding species (Silva and Casteleti, 2005). The most common families are Fabaceae-Papilionoideae (49 species), Myrtaceae (45 species), Annonaceae (27 species), Euphorbiaceae (22 species), Sapindaceae (18 species), Malvaceae (17 species), Rutaceae (17 species), Melastomataceae (15 species), Apocynaceae (15 species), and Burseraceae (9 species) (Lôbo et al., 2011). Pollen indicators for Atlantic Forest montane enclaves are represented by *Guapira-Pisonia* (Nyctaginaceae), *Clusia* (Clusiaceae), *Zanthoxylum* (Rutaceae), Spermacoceae, and Araceae (Montade et al., 2019).

2.4. Caatinga

The Caatinga is located in the eastern and central region of NEB, extending across more than 800,000 km^2 of the region's states (53 % of the NEB area), except in the Maranhão (Fig. 2) (Moro et al., 2016). It is a dry forest characterized by sparse deciduous thorny vegetation, with small trees and shrubs, well adapted to the hot, semi-arid climate and a short rainy season from January to May (3–5 months) (Nimer, 1989); mean annual temperature is 28 °C and mean annual precipitation varies from 400 to 800 mm (INMET, 2023). The peak of the rainy season corresponds to the ITCZ southern position between February and May (Marengo et al., 2017). The Caatinga tolerates interannual precipitation variability and recurrent drought events (Moro et al., 2016). Including woody and herbaceous strata, the richest families are Fabaceae (292 species), Euphorbiaceae (103 species), Malvaceae (82 species), and Asteraceae (67 species) (Moro et al., 2014). The ten most common genera are *Croton* (Euphorbiaceae) (37 species), *Mimosa* (Fabaceae) (28 species), *Ipomoea* (Convolvulaceae) (28 species), *Chamaecrista* (Fabaceae) (24 species), *Erythroxylum* (Erythroxylaceae) (24 species), *Senna* (Fabaceae) (21 species), *Cyperus* (Cyperaceae) (20 species), *Eugenia*

(Myrtaceae) (19 species), *Sida* (Malvaceae) (17 species), and *Evolvulus* (Convolvulaceae) (16 species) (Moro et al., 2014). Caatinga pollen indicators are represented by assemblages of *Mimosa* (Mimosoideae), *Combretum* (Combretaceae), *Zizyphus* (Rhamnaceae), *Althernantera* (Amaranthaceae), *Borreria* (Rubiaceae), and *Mitracarpus* (Rubiaceae) (Ledru et al., 2020).

2.5. Cerrado

The Cerrado extends over the western/southwestern regions of Bahia, Maranhão, Piauí, and north of Maranhão and Piauí states (Fig. 2), occupying some 465,500 km^2 (30 % of the NEB area) (IBGE, 2021). The climate is tropical seasonal, with a rainy season from October to March (5–6 months), annual temperature ranges from 22° to 27 °C, and mean annual precipitation varying between 1000 and 1800 mm (Silva et al., 2008). Its location between the dry Caatinga and the Amazon moisture flux (Castro et al., 1998), and the latitudinal range of 2°–15°S entails significant variability in the onset and duration of the rainy season and mean temperatures (Castro and Martins, 1999). In the north (5–2°S), the rainy season corresponds to the ITCZ southern position between February and May (4–5 months), while in the southwest (15–5°S) it is modulated by the SAMS, from October to March (5–6 months). However, the duration of the rainy season can be shortened by up to four months during years with drought episodes in some Cerrado areas of southern Maranhão and Piauí (Silva et al., 2008). In these areas, the mean minimum temperature ranges from 21° to 23 °C, while the mean maximum varies between 31° and 33 °C (Silva et al., 2008). The Cerrado includes dry and moist forests, woody savannas, palm swamps, and grasslands, differing floristically from the core region in Central Brazil (Ratter et al., 2011). In NEB, the ten most common genera are *Qualea* (Vochysiaceae), *Byrsonima* (Malpighiaceae), *Anacardium* (Anacardiaceae), *Bowdichia* (Fabaceae), *Annona* (Annonaceae), *Caryocar* (Caryocaraceae), *Dimorphandra* (Fabaceae), *Hymenaea* (Fabaceae), *Stryphnodendron* (Fabaceae), and *Curatella* (Dilleniaceae) (Vieira et al., 2019). In Central Brazil, the ten most common genera are *Paepalanthus* (Eriocaulaceae), *Mimosa* (Fabaceae), *Chamaecrista* (Fabaceae), *Myrcia* (Myrtaceae), *Hyptis* (Convolvulaceae), *Vellozia* (Velloziaceae), *Croton* (Euphorbiaceae), *Syngonanthus* (Eriocaulaceae), *Xyris* (Xyridaceae), and *Paspalum* (Poaceae) (Mendonça et al., 2008). Thus, the NEB Cerrado is classified as a peripheral province with a unique species assemblage, set apart from those of Central Brazil (Françoso et al., 2019; Ratter et al., 2003; Vieira et al., 2019). This provincialism is attributed to the geographic dispersal, climate variability, and intermixing of species from both Caatinga and Amazon vegetation (Castro and Martins, 1999; Vieira et al., 2019).

Palm swamp (*vereda* in Portuguese) is a type of wetland typical of Cerrado, widely found within the biome (Ribeiro and Walter, 2008). It is characterized by herbaceous-subshrub strata with the presence of the palm tree *Mauritia flexuosa* (Arecaceae) (da Silva et al., 2018) on flooded soils under a warm climate, usually below 1000 m elevation (Rull and Montoya, 2014). *Mauritia* swamp communities possess high floristic richness that differs from each other, harboring exclusive species and a distinguished flora when compared to other Cerrado physiognomies (da Silva et al., 2018). *Mauritia* swamps can be widely found in the Cerrado of Bahia, Piauí, and Maranhão states (Barroso and Guimarães, 1980; SpeciesLink, 2024), with occurrences in the rainforest of Maranhão state (Araujo and Pinheiro, 2012) and at the Araripe plateau of the Ceará state (Guerra et al., 2020). Assemblages of Cerrado pollen indicators are composed of *Caryocar* (Caryocaraceae), *Curatella* (Dilleniaceae), *Byrsonima* (Malpighiaceae), *Borreria* (Rubiaceae), and *Didymopanax* (Araliaceae) (Oliveira and Marquis, 2002), while *Mauritia* is the key indicator of palm swamps (Cassino and Ledru, 2021).

2.6. Ecotones and transition areas

The transition between the Caatinga and Cerrado (*Carrasco* in Portuguese) is characterized by a dense shrubland with xerophytic vegetation, vines, and sparse trees (Araújo and Martins, 1999). The *Carrasco*'s most common species are *Aspidosperma pyrifolium* (Apocynaceae), *Byrsonima blanchetiana* (Malpighiaceae), *Chloroleucon foliolosum* (Mimosoideae), *Mimosa acutistipula* (Mimosaceae), *Piptadenia moniliformis* (Mimosaceae), *Passiflora foetida* (Passifloraceae), *Guettarda angelica* (Rubiaceae), *Allophylus quercifolius* (Sapindaceae), and *Solanum baturitense* (Solanaceae) (Araújo et al., 1998, 1999; Castro et al., 1998).

In the transition areas between the NEB Cerrado and Amazon, the most common species are *Himatanthus articulates* (Apocynaceae), *Bauhinia macrostachya* (Fabaceae), *Exellodendron gardneri* (Chrysobalanaceae), *Platonia insignis* (Clusiaceae), *Enterolobium schomburgkii* (Fabaceae), *Parkia platycephala* (Fabaceae), *Plathymenia foliolosa* (Fabaceae), *Brosimum guianensis* (Moraceae), *Virola surinamensis* (Myristicaceae), and *Pouteria ramiflora* (Sapotaceae) (Castro et al., 1998). Due to the species intermixing between biomes, the ecotones show higher levels of diversity in comparison to the biome's core domain (Castro et al., 1998), making NEB one of the South America's most important centers of endemism and biodiversity (Da Silva and Tabarelli, 2000; Ratter et al., 2011). *Carrasco* pollen indicators are *Magonia* (Sapindaceae), *Callisthene* (Vochysiaceae), *Dilodendron* (Sapindaceae), and *Terminalia* (Combretaceae), while for the Cerrado–Amazon transition, pollen indicators are *Hirtella* (Chrysobalanaceae), *Emmotum* (Metteniusaceae), *Vochysia* (Vochysiaceae), and *Sclerolobium* (Fabaceae) (Oliveira and Marquis, 2002).

2.7. Fire regimes

All of the NEB biomes are subjected to fires, from natural to anthropogenic in character to a greater or lesser degree. Natural fires are common in the Cerrado during the transition from dry to rainy season, because of the recurrent frequency of lightning and the ready availability of continuous flammable fuel (Gomes et al., 2018). The Cerrado is in fact a highly fire-prone biome (Hardesty et al., 2005) with a large number of species whose life cycles depend on seasonal fire regimes (Simon and Pennington, 2012). However, natural fires are rare in the Caatinga and both the Amazon and Atlantic rainforests. The former because of the low frequency of lightning and the sparse vegetation hindering continuous burning (Pivello et al., 2021) – which classifies the Caatinga as a fire-independent biome (Hardesty et al., 2005) – whereas in the latter the high moisture content prevents ignition and propagation (Pivello et al., 2021). However, the Amazon Forest can become more susceptible to fires during extreme drought events (Silva-Junior et al., 2020). Thus, the Amazon and Atlantic rainforests are classified as fire-sensitive biomes (Hardesty et al., 2005) composed of species lacking evolutive adaptations to fire disturbance.

In contrast, anthropogenic fires are frequent in all of the four NEB biomes (Pivello, 2011), with a gradient of local fires from the coast to the interior of the region associated to changes in land use practices (de Oliveira-Júnior et al., 2022). Today, fire is used to remove natural vegetation for extensive agriculture and cattle ranching in the Amazon Forest and Cerrado (Pivello, 2011), while the Caatinga undergoes slash-and-burn itinerant agriculture and considerable charcoal production by rural communities (Araujo et al., 2023; Mamede and de Araújo, 2008). The greatest occurrence of fires in Caatinga is located in the ecotones with the Cerrado (Argibay et al., 2020; Martins et al., 2024). Most burnings in the Cerrado–Caatinga transition and Atlantic Forest are related to agricultural consortia MATOPIBA (an acronym for the states of **MA**ranhão, **TO**cantins, **PI**auí and **BA**hia) and SEALBA (an acronym for the states of **SE**rgipe, **AL**agoas, and **BA**hia), respectively (de Oliveira-Júnior et al., 2022).

2.8. Human activities

Hosting more than 54 million people, NEB's human population density is 35 inhabitants/km^2 (IBGE, 2022a). Due to heterogeneity of vegetation, soil types, and climate, different human activities are practiced in each biome. In the Amazon Forest and Cerrado are found illegal logging, human-created pastures, the general expansion of agricultural frontiers, and cattle ranching (Silva-Junior et al., 2020, 2022). In Caatinga, subsistence farming of forage palm, corn, beans, and manioc for self-consumption by rural families and regional market sales are the main land use practices (INSA, 2023). In the Atlantic Forest, human activities comprise deforestation for the production of sugarcane, fruits, tobacco, manioc crops, and the creation of pasturelands (Lins-e-Silva et al., 2021). In total, NEB has approximately 10 million hectares of agricultural land (CONAB, 2024), with 90 % of grain production being farmed on the MATOPIBA region, a Cerrado–Caatinga ecotone (Araújo et al., 2019).

3. Methods

We first selected 13 studies consisting of pollen records (Table S1). A set of criteria was used to ensure comparability in chronologies between the different records. We considered: 1) only peer-reviewed published studies, 2) minimum duration of record $\geq$500 years, 3) temporal resolution $\leq$100 years, and 4) no age inversions and continuous deposition (no sedimentary hiatus). Studies suitable by criteria but with summarized presentation of pollen data were excluded from our discussion. Furthermore, we considered a more flexible temporal resolution depending on the relevance of the study within the regional climate framework (Table S1.). Therefore, from the 13 published studies, nine pollen records (Table 1 and Fig. 2) were selected. Records were assigned into two groups based on the location of sites within the current east–west precipitation gradient (Fig. 1a): western NEB (west of 42°) and eastern NEB (east of 42°) (Table 1). To observe environmental changes through time, we built synthetic pollen diagrams (Fig. 4c) with the most representative taxa from each site (Table S2), using data available in the Latin American Pollen Database (Flantua et al., 2015) and from authors who responded favorably to our requests for information. Based on the observed major changes in the vegetation reconstructed with the pollen assemblages and hierarchical clustering using the CONISS method (Grimm, 1987), four time periods were assigned: 6.0–5.2 ka BP, 5.2–4.2 ka BP, 4.2–2.6 ka BP, and 2.6–0.0 ka BP (Fig. 3). The environmental interpretation was based on the description of pollen assemblages from the most representative taxa (Table S2) that categorized the vegetation during the Holocene in each record, considering the response of the different vegetation types to climate changes that occurred during each period. Then, a vegetation gradient was built based on the pollen assemblages that represent a vegetation physiognomy within the biome: rainforest, arboreal cerrado, open cerrado, and caatinga (Fig. 3a and b). Pollen records were then compared to moisture balance (precipitation minus evaporation) based on the oxygen isotope variations ($\delta^{18}O$) from speleothem records on the eastern NEB within the Caatinga (Cruz et al., 2009; Utida et al., 2020), on the southern NEB boundary with Cerrado (Stríkis et al., 2011), and on the percentages of rainforest taxa from a pollen record on the western NEB boundary with the Amazon Forest (Hermanowski et al., 2012) (Fig. 3c).

All pollen records, except the one from Serra do Maranguape (Montade et al., 2014), also included charcoal analyses (Table 1), consisting of three methods: macro-charcoal analyses (>160μ) based on the abundances and morphology of particles (Umbanhowar and McGrath, 1998) combined with statistical *CharAnalysis* (Higuera et al., 2010), and micro-charcoal analyses (<160μ) based on the abundances of charred particles in the pollen slides (Tolonen, 1986). All of these techniques aimed to reconstruct fire occurrences and decipher how they changed at each site. Prior to comparing fire activity, we verified the suitability of each macro-charcoal record for peak identification calculating a signal-to-noise index (SNI>3, Kelly et al., 2011) (see supplementary material) within the *CharAnalysis* (Higuera et al., 2010), using the charcoal data available in the Global Paleofire Database (https://www.paleofire.org/index.php). Then, we interpolated the charcoal data to minimum 15-year time steps to approximate the mean sample resolution of all sites, and decomposed to a background trend using a moving median (with a 400-year smoothing window) and evaluated peak samples with a Gaussian mixture model and threshold values (see supplementary material). This step was taken to reduce biases in the fire detection due to variability in sampling resolution within and between records (Higuera et al., 2010). Based on the peak magnitude, temporal pattern of identified charcoal peaks, and changes in the charcoal accumulation rate, we inferred shifts in fire activity as a reflection of climate variability or human influence (Pausas and Keeley, 2009; Vachula et al., 2021). Periods with low charcoal deposition and peak magnitude suggest reduced fuel consumption, interpreted as reduced burnings, while charcoal peaks and elevated charcoal deposition reflect changes in local fires, interpreted as more availability of fuel and increased burnings

Table 1

List of the nine pollen records selected according to their age, temporal resolution, and relevance in the study area. A star-shaped mark (*) indicates records that also include charcoal analyses.

Site name and reference	Location	Vegetation	Coordinates	Archeological sites with reference
1. Chapada das Mesas (Xavier et al., 2024)*	South of Maranhão, western NEB	Cerrado–Amazon ecotone	7°S–47°W, 307m aslc	Chapada das Mesas (ICMBio, 2019)
2. Cabeludo (Moraes et al., 2022)*	Northern coast of Maranhão, western NEB	Amazon rainforest with marine influence	2°S–45°W, 4m asl	Cabeludo (Navarro, 2018)
3. Lake Formoso (Moraes et al., 2021)*	Northern coast of Maranhão, western NEB	Amazon rainforest with marine influence	3°S–45°W, 3–10m asl	Encantado, Formoso, Caboclo, Boca do Rio (Davis and Navarro, 2023; Navarro, 2018)
4. Lake Caço (Ledru et al., 2006)*	Northern coast of Maranhão, western NEB	Cerrado	2°S–43°W	Absent
5. Icatu Valley (Oliveira et al., 1999)*	North of Bahia, western NEB	Caatinga	10–11°S 42–43°W, 800m asl	Abrigo Pilão, Toca da Esperança, São Raimundo Nonato (Martin, 2013; Souza et al., 2020)
6. Sete Cidades (Xavier et al., 2022)*	North of Piauí, eastern NEB	Cerrado–Caatinga ecotone	4°S–41°W, 100–290m asl	Pedra do Cantagalo I (Cavalcante, 2018)
7. Araripe (Guerra et al., 2024)*	South of Ceará, eastern NEB	Evergreen forest	7°13′52.69″S– 39°28′30.83″W and 7°24′27.96″S–39°12′10.40″W, 737–763m asl	Anauá, Araripina, Baixio dos Lopes, Baixio dos Caboclos, Exu, Pedra do Caboclo (Martin, 2013; Souza et al., 2020)
8. Catimbau (Moraes et al., 2020)*	East of Pernambuco, eastern NEB	Caatinga	8°S–37°W, 200–727m asl	Buíque, Catimbau, Chã do Caboclo (Martin, 2013; Souza et al., 2020)
9. Serra do Maranguape (Montade et al., 2014)	North of Ceará, eastern NEB	Ombrophilous montane forest	3°S–38°W, 900m asl	Absent

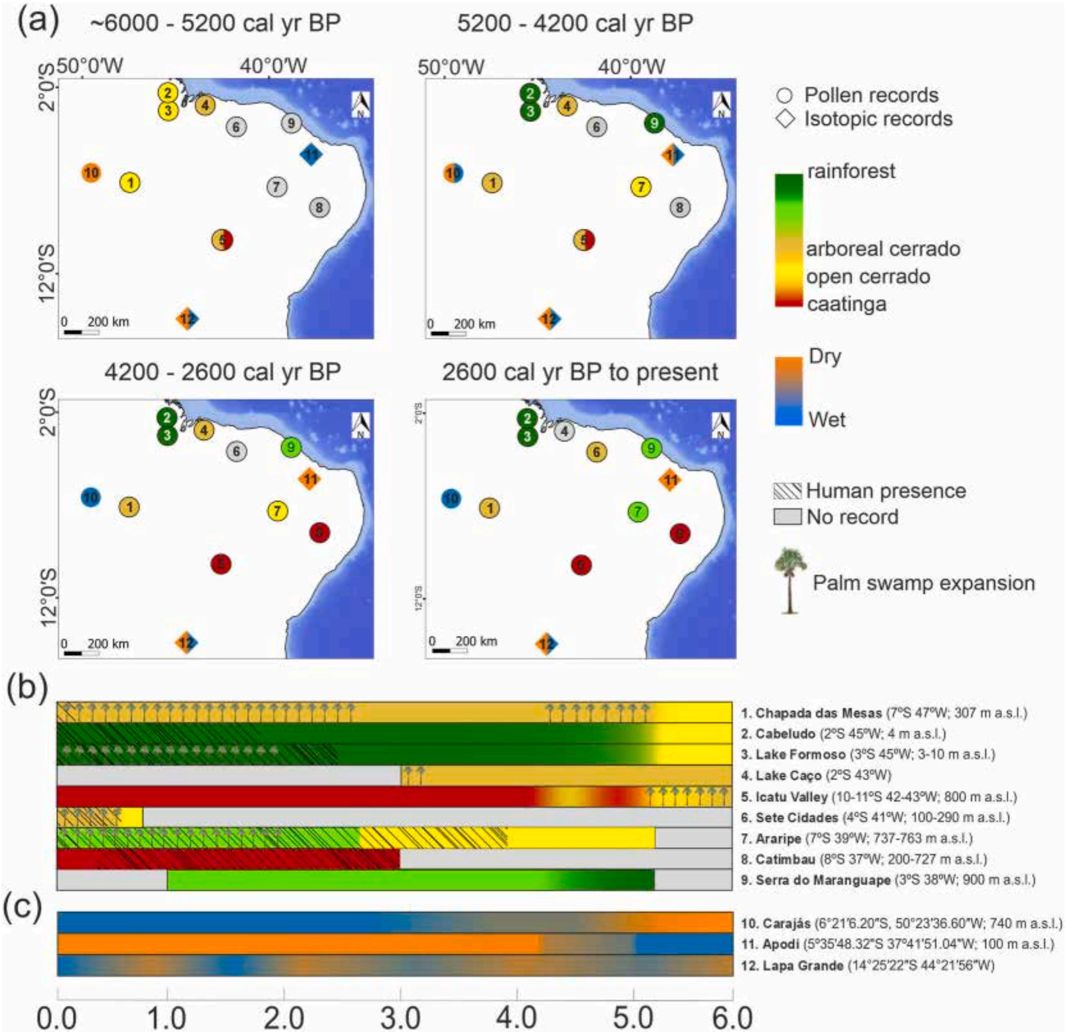

Fig. 3. a) Graphic representation of the changes observed in vegetation and climate records for the four time windows discussed in the text. b) Summary of vegetation changes based on the interpretation of the pollen records. Hatching indicates human presence. *Mauritia* expansions are indicated by the palm tree. c) Summary of moisture balance based on sedimentological and isotopic records (see 3. Methods section).

(Higuera et al., 2010). We then assigned an intensity signal of high fire activity (values above the defined threshold), and low fire activity (values below the defined threshold) for each site during the last 6000 years. By using the *CharAnalysis*, the macro-charcoal (pieces/cm^3) were multiplied by the estimated sedimentation rate (cm/yr) to obtain the charcoal accumulation rate (number of pieces/cm^2/yr^1) of each sample (CHARa, Fig. 4c). Micro-charcoal results from pollen slides were presented as in their respective published papers (Fig. 4c).

For records with micro-charcoal analysis carried out on pollen slides and records with unavailable databases, we based the intensity fire signal on the description and interpretation of each study. For the discussion of fire activity, we discussed charcoal data from soil pit records from Sete Cidades and Araripe Forest, both Cerrado–Caatinga ecotones (Pessenda et al., 2010). To avoid overinterpretation of sites that may have poor chronologies, we recalibrated all ages of each site to IntCal series in the Calib 8.20 software (SHCal20 curve for the Southern Hemisphere) (Hogg et al., 2020), then we built age-depth models using the *Rbacon* package (Blaauw and Christen, 2011) in RStudio. Serra do Maranguape (Montade et al., 2014), Lake Caço (Ledru et al., 2006), and Icatu Valley (Oliveira et al., 1999) showed a different chronology than in the published paper (Table S3). Thus, the interpretation and discussion were based on the recalibrated dates. We also considered the geographical settings of each record for the paleoecological comparisons between sites in the discussion.

To provide accurate evidence of human activity in each site, we sought to observe three specific things in the pollen records: a sharp decrease of arboreal taxa, the presence of crop indicator taxa, and intervals showing high CHARa. Pollen indicators of human activity were assigned to two classes: direct indicators that provide clear evidence of land use (e.g. the presence of crops such as *Phaseolus*, *Zea mays*, *Manihot*), and indirect indicators (e.g. pioneer taxa indicators of deforestation such as *Cecropia*, *Vismia*, and palm trees *Mauritia*, *Euterpe*) (Table S2) (Flantua et al., 2016), that is taxa which also occur naturally in the vegetation. When confronted with indirect indicators, the inference for human activity was further investigated based on changes in pollen spectra with the appearance of disturbance-related taxa combined with charcoal and archeological data.

4. Results

A comparison of the vegetation changes and fire activity between sites allows us to draw a general pattern of climate changes in the western and eastern NEB during four distinct time intervals: 6.0–5.2 ka BP, 5.2–4.2 ka BP, 4.2–2.6 ka BP, and 2.6–0.0 ka BP, (Figs. 3 and 4).

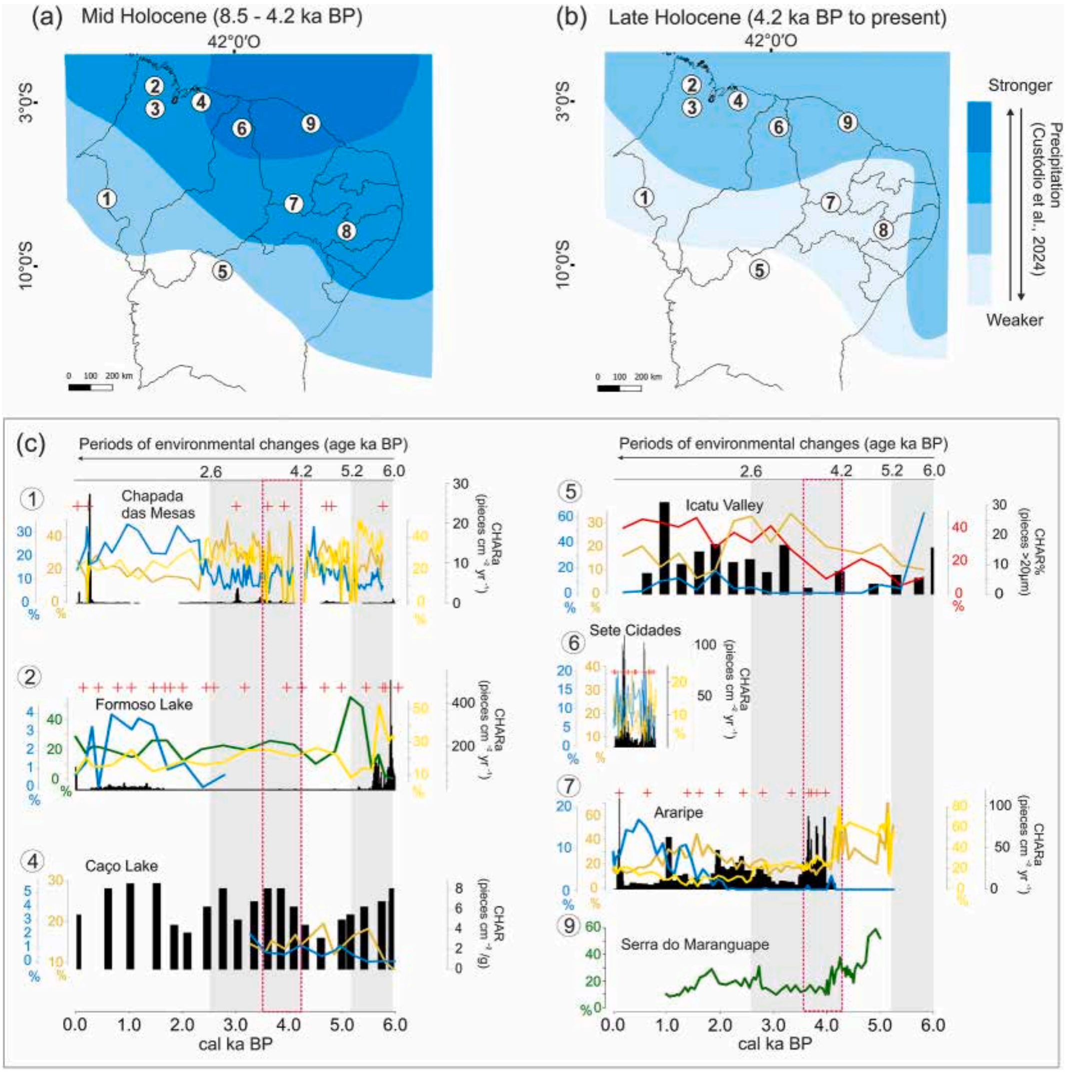

Fig. 4. 6000 years of vegetation changes in eastern and western NEB. Spatial precipitation variability from TraCE-21k simulations for a) Mid Holocene and b) Late Holocene (Custódio et al., 2024). c) synthetic diagrams of the most representative pollen taxa from each record associated to different vegetation types: rainforest (dark green line); arboreal cerrado (light brown line); open cerrado (yellow line); xerophilous caatinga (red line). The blue lines show the percentages of *Mauritia flexuosa*. Black bars show charcoal accumulation from macro-charcoal records, CHARa (pieces cm $^{-2}$ yr $^{-1}$), and micro-charcoal records (particles area cm $^{-2}$/g and particles % > 20 μm). Fire events are represented by a red cross. Our four intervals of regional environmental changes are highlighted with gray/white shaded areas. The "4.2 dry event" is pink dashed: from ~4.3 to 3.6 ka BP in Chapada das Mesas (pollen-poor sediments), from 4.2 to 3.5 ka BP in Serra do Maranguape (decrease of montane ombrophilous forest), and after 4.2 ka BP in Icatu Valley (expansion of caatinga). See Fig. 1 for site locations.

5. Discussion

5.1. *Vegetation changes in NEB were driven by an east–west rainfall gradient*

We found a strong vegetation-climate correlation within the qualitative reconstructions and pollen data used in our analysis, indicating that vegetation responded to precipitation changes across NEB, with some sites responding differently depending on the position of the air masses. Between 6.0 and 5.2 ka BP, open vegetation with rare tree cover was dominant in most of the western NEB sites (Fig. 4c, 5 ab), suggesting an overall precipitation decrease in the region apart from the records of Lake Caço and Icatu Valley with a woody cerrado and a palm swamp, respectively (Fig. 4c, 5a). The presence of an arboreal cerrado at Lake Caço and at Icatu is likely due to their geographical location (Fig. 5a) outside the moisture band highlighted by TraCE-21k simulations (transient climate evolution of the last 21,000 years – Last Glacial Maximum to present) (Custódio et al., 2024) (Fig. 4a) and influenced by local humidity variations. Because the Icatu Valley is centrally located within the NEB considering the 42° west/east groups (Fig. 2) and exhibits more similarity to the eastern NEB (Fig. 4c), we have discussed the Icatu site accordingly.

Eastern NEB recorded wetter conditions than today (Gorenstein et al., 2022; Utida et al., 2020), while precipitation oscillated in western NEB (Figs. 5 and 6a). The humidity gradient established from east to west across the region contrasts with the rest of South America and Central Brazil (Stríkis et al., 2011; Wang et al., 2007), where weakened monsoon convection and decreased rainfall prevailed (Prado et al., 2013). This occurred because precession-induced configuration caused a minimum austral summer insolation, creating a strong interhemispheric SST gradient due to the slower response of the South Hemisphere tropical sea surface to insolation changes compared to that of the North Hemisphere (Campos et al., 2022). Results from the TraCE-21k models showed a direct connection between warming of the North Atlantic, which could be associated to a strong northward Atlantic Meridional Overturning Circulation (AMOC) heat transport, and a northward ITCZ shift during the MH (Custódio et al., 2024; Gorenstein et al., 2022). Furthermore, speleothem records from across the SAMS region also

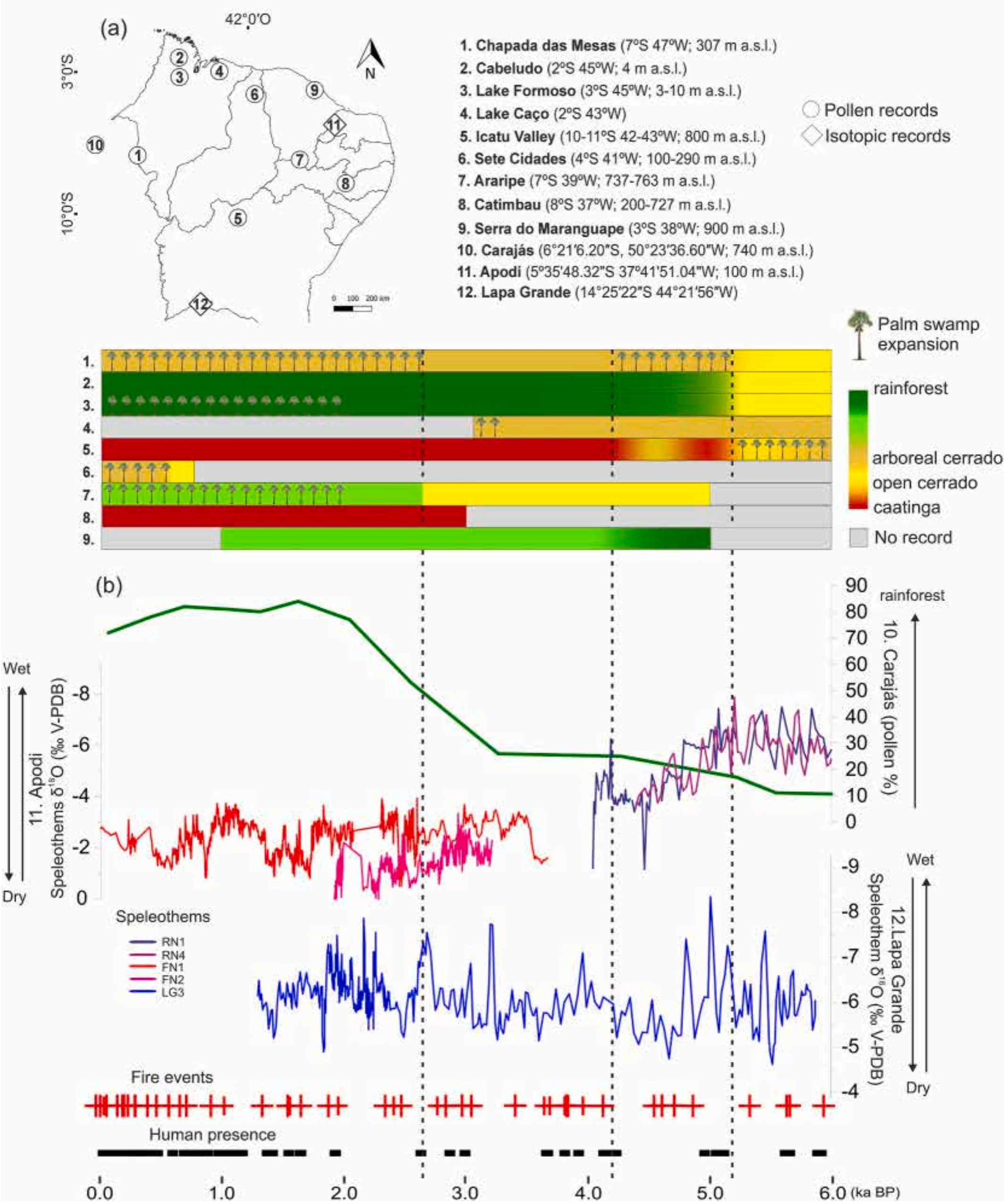

Fig. 5. Summary of 6000 years vegetation and climatic changes in NEB. a) Summary of vegetation changes based on the interpretation of the pollen records for the four time intervals (vertical dashed lines). *Mauritia* expansions are indicated by the palm tree. b) Pollen data from Carajás (Hermanowski et al., 2012), and isotopic data from Apodi (Cruz et al., 2009; Utida et al., 2020, 2023), and Lapa Grande (Stríkis et al., 2011). Fire events based on the analyses of macro-charcoal data available in the pollen records are represented by red crosses. Human occupation near the pollen sites is based on radiocarbon dates (Table S4).

showed a spatiotemporal heterogeneity linked to variations in local humidity and karst conditions (Cruz et al., 2009; Utida et al., 2020).

From 5.2 to 4.2 ka BP, the expansion of woody cerrado and arboreal rainforest taxa in western NEB and the predominance of moist forest in eastern NEB (Figs. 3a and 4c) suggest overall increased temperatures and precipitation levels in most of the region. However, two eastern sites were antiphased: Icatu Valley, where a decrease of *Mauritia* and variations of arboreal/herbaceous cerrado and caatinga taxa (Figs. 4c and 5a) indicate moisture fluctuations in the palm swamp; and the Araripe, where an open vegetation with scarce trees and predominant herbs (Fig. 4c) characterized drier-than-today conditions. This wetter interval, also observed over the Amazon and Central Brazil (Stríkis et al., 2011), relates to the increasing Southern Hemisphere summer insolation (Berger and Loutre, 1991) which induced warmer South Atlantic SSTs and a southernmost ITCZ position (Utida et al., 2020). This led to a strengthened SACZ convection in southwestern NEB and higher sea level locally (Caldas et al., 2006; Suguio et al., 2013). Increased precipitation over NEB is also connected to insolation decrease in the Northern Hemisphere, freshwater pulses in the North Atlantic Ocean, and a decrease of greenhouse gases (Custódio et al., 2024). Between 5.2 and 4.2 ka BP, the increase of rainfall favored the expansion of palm swamp and woody cerrado in the southwestern inland region, of Amazon rainforest taxa and mangroves on the western coastal region, and a predominance of ombrophilous forest in the eastern montane (Fig. 3b and 4c). The variations observed at Icatu (Fig. 5a) are explained by its location on the boundary of the SAMS influence but still under the ITCZ domain whose southern incursions over NEB are influenced by the intensity and position of the South Atlantic Subtropical High (Custódio

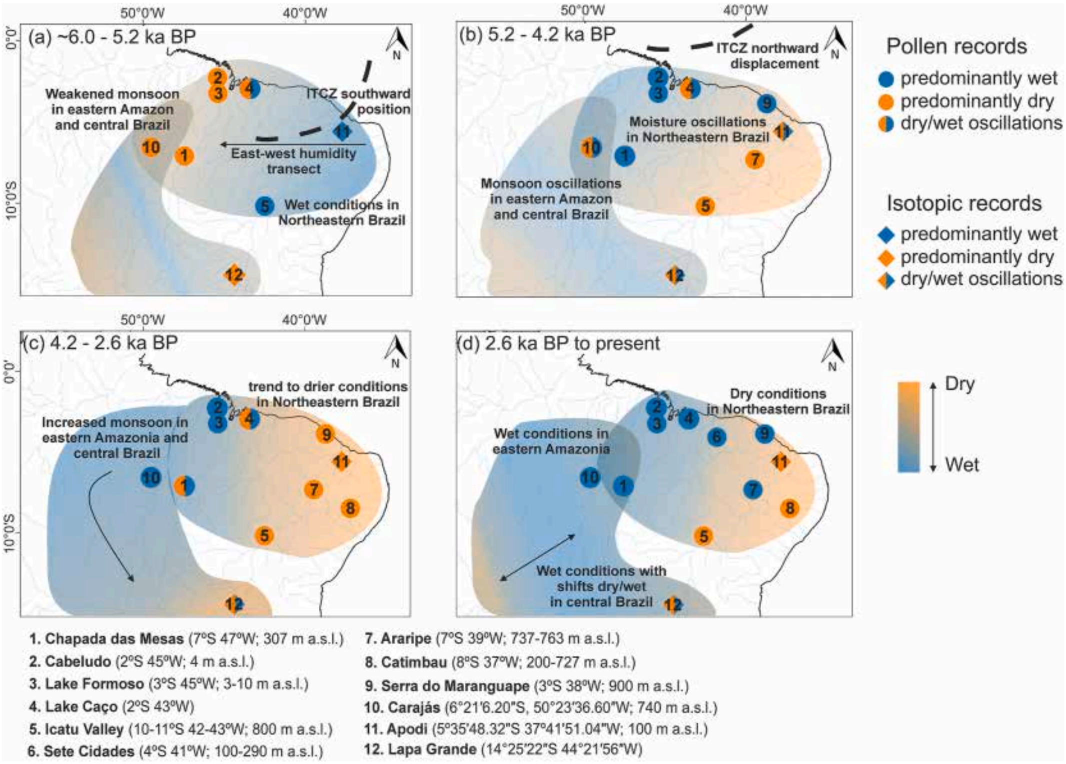

Fig. 6. Schematic reconstruction of 6000 years of SAMS activity and ITCZ associated east–west moisture gradient based on pollen (Table 1) and isotopic/pollen records (see Methods section) discussed in the text for the four considered time intervals. a) ~6.0–5.2 ka BP; b) 5.2–4.2 ka BP; c) 4.2–2.6 ka BP; d) 2.6 ka BP to present.

et al., 2024; Gorenstein et al., 2022). Because the east-west humidity transect is not a straight line, antiphased records reflect the variability of the monsoon moisture convection and the shifting of convergence zones over the NEB, as modeled in the TracCE-21k reconstruction (Custódio et al., 2024) (Figs. 4a and 6b). Moreover, paleorecords indicate a transition of environmental conditions between 5.0 and 4.2 ka BP in the region (Utida et al., 2020) due to a warmer SST in the North Atlantic that caused the ITCZ northward shift (Custódio et al., 2024). The predominant open vegetation in Araripe suggests that it is located outside the monsoon convection, reflecting low rainfall due to oscillations in the position of the moisture band, which also affected the aquifer resurgence (Guerra et al., 2024). Such variability was also observed in isotopic records, for example the absence of speleothems deposition in Apodi (Utida et al., 2020), which indicates lower rainfall than previously recorded. Furthermore, the northeastern coast of Brazil experienced higher moisture levels during the MH compared to today, while the region at the boundary between NEB and central/southeastern Brazil exhibited inconsistent rainfall patterns (Gorenstein et al., 2022). This suggests a localized, erratic rainfall regime with periods of increased moisture, likely due to altered precipitation patterns over the SACZ and a weaker South Atlantic Subtropical High during the MH.

From 4.2 ka BP onwards, we observed the expansion of Caatinga xerophilous vegetation over a period of ~300 years (Moraes et al., 2020; Oliveira et al., 1999), a change in the structure of montane forest in Maranguape (Fig. 3ab, 4c), from a dense ombrophilous forest to a semi-deciduous forest over a period of ~100 years (Montade et al., 2014), and persistence of an open landscape with sparse cerrado trees that lasted ~1400 years (Fig. 3ab, 4c) (Guerra et al., 2024). Most of the western NEB sites show no vegetation changes at ~4.2 ka BP (Fig. 4c), with the exception of Chapada das Mesas, where low pollen concentration samples between ~4.3 and 3.6 ka BP, interpreted as a result of low edaphic moisture conditions which induced an oxidation of the pollen content (Xavier et al., 2024), were followed by a predominance of dry-adapted cerrado trees (Fig. 4c). Woody cerrado and Amazon rainforest trees that started to expand circa 5.2 ka BP became established at 4.2 ka BP in the western coast, while arboreal cerrado gradually expanded in the southwest inland after an increase in moisture conditions around 3.5 ka BP (Figs. 3b and 4c). These vegetation changes are in agreement with the climatic records which show dry conditions recorded over eastern NEB (Utida et al., 2020) and wet conditions in the western region (Hermanowski et al., 2012, 2015) due to amplified summer insolation and higher ITCZ variability (Utida et al., 2020, 2023). A strengthened monsoon activity marked the LH in Central Brazil (Stríkis et al., 2011) and the eastern Amazon (Hermanowski et al., 2012; Sifeddine et al., 2001), influencing the vegetation over the western NEB boundary (Figs. 5 and 6c).

The "4.2 ka event" is one of the most remarkable climate events of the Holocene and marks the current chronostratigraphic base of the Late Holocene. Models suggest that a warm Pacific SST and cold Atlantic SST produced a decrease in precipitation in west and east Africa and increased precipitation in tropical South America (Renssen, 2022). In NEB, the 4.2 ka BP marks the onset of aridification (Utida et al., 2020) (Figs. 5 and 6c), similar to west/east Africa and in contrast to the wet climate for the rest of tropical South America (Cruz et al., 2009; van Breukelen et al., 2008). Hydroclimate reconstructions revealed that this NEB/SAMS climate dipole has operated on both orbital (Campos et al., 2022) and millennial cycles (Choblet et al., 2024) under a combination of insolation forcing, thermal variability of intertropical Atlantic SST, and Walker atmospheric circulation (Custódio et al., 2024). This pattern is related to the ITCZ interhemispheric shifts, associated with changes in the Atlantic Ocean thermal gradients (Wainer et al., 2021) and associated Hadley cell intensity which affects monsoon convection over South America and NEB precipitation (Custódio et al., 2024; Novello et al., 2018). Thus, our study shows that gradual changes in this dipole behavior during the last 6000 years affected the regional vegetation, splitting the region into two climatic subregions with zonal phases of biome retraction and expansion. Moreover, the 4.2 ka dry event in NEB broadly affected the vegetation composition of eastern montane forests and western woody cerrado, both taking more than 100 years to recover from such disturbance (Montade et al., 2014; Xavier et al., 2024).

After 2.6 ka BP, woody cerrado, gallery forest, and palm swamp expanded in southwestern NEB, while rainforest vegetation and palm trees dominated the northwestern coastal region (Fig. 3ab, 4c). The caatinga dry forest predominated throughout most of the eastern landscapes, except for the two forest refugia where an ombrophilous montane forest (Montade et al., 2014) and an expansion of palm swamp and evergreen forest trees in response to increased groundwater resurgence in the Araripe plateau (Guerra et al., 2024) was observed. This pattern indicates the installation of a bimodal climate with a dry eastern/wet western NEB (Fig. 5b and 6d) as observed today (Fig. 1a).

5.2. Changes in fire activity and links with human presence

NEB is rich in archeological sites with scarce radiocarbon dating in comparison to Central and Southern Brazil. Here, the demographic dynamics of the region were evaluated and compared with the multiproxy data. While the sparse radiocarbon dates between 6.0 and 4.2 ka BP limit interpretations, chronologies from 4.2 ka BP onwards allow for some inferences about the human influence based on fire activity (Power et al., 2008).

From 6.0 to 4.2 ka BP, fires in Lake Formoso (Moraes et al., 2021), Cabeludo (Moraes et al., 2022), Lake Caço (Ledru et al., 2006), Icatu Valley (Oliveira et al., 1999), Chapada das Mesas (Xavier et al., 2024), and Araripe (Guerra et al., 2024) (Figs. 4c and 7) were associated to climate variability. However, this connection is debatable for some sites. At Lake Formoso (Moraes et al., 2021), no direct correlation was made between high fire activity and human presence, even considering archeological evidences of such dating back to ~6600 cal yr BP in the Maranhão lowlands (Davis and Navarro, 2023). This contrasts with the low fire activity at the Cabeludo site (Moraes et al., 2022), ~130 km distant (Fig. 3a and b). At Lake Caço, climate-induced fires were attributed to burning of the herbaceous layer as the Cerrado arboreal taxa started to expand (Ledru et al., 2006). Although hunter-gatherer groups were recorded in the northern coastal area of Maranhão during the mid-late Holocene (Bandeira, 2009, 2013), the lack of evidence in the pollen record and absence of archeological sites combine to limit further conclusions. At Icatu Valley, it has been suggested that charcoal fragments (Fig. 4c) are from natural fires. However, it is possible that those fires were of an anthropogenic character rather than climatic, once anthropogenic activity becomes the primary cause of fires in the Caatinga (Pivello et al., 2021). Radiocarbon dates from central Bahia point to a human presence since, at least, 6.0 ka BP (Martin, 2013) (Fig. 7), but no further evidence was observed in the pollen record. *Mauritia* is recorded during this period but declines abruptly around 5.2 ka BP (Fig. 4c), likely responding to a precipitation decrease. In the western cerrado of Chapada das Mesas, the low fire activity from 6.0 to 4.2 ka BP (Fig. 4c and 7) was first related to drier-than-today conditions followed by a wetter climate (Fig. 6b) (Xavier et al., 2024). In eastern cerrado refugia, at Araripe, the low fire frequency was a result of environmental conditions related to limited availability of fuel and the distance from the fuel source and the deposition site (Guerra et al., 2024). In NEB, climate variability was attributed to local demographic shifts, possibly causing oscillations in the archeological signal as human groups would migrate only a few kilometers away (Araujo et al., 2025). This could explain the discrepancies between the archeological record and fire activity between Lake Formoso and Cabeludo, as well the differences observed in Icatu Valley and Lake Caço.

Interestingly, the last 4000 years showed an increase in fire activity in eastern NEB, with some variability in the western sites (Fig. 7). Climate-induced fires are characterized as surface fires ignited by lightning strikes that consume the herbaceous strata accumulated during the wet season and becoming flammable during the dry season; they

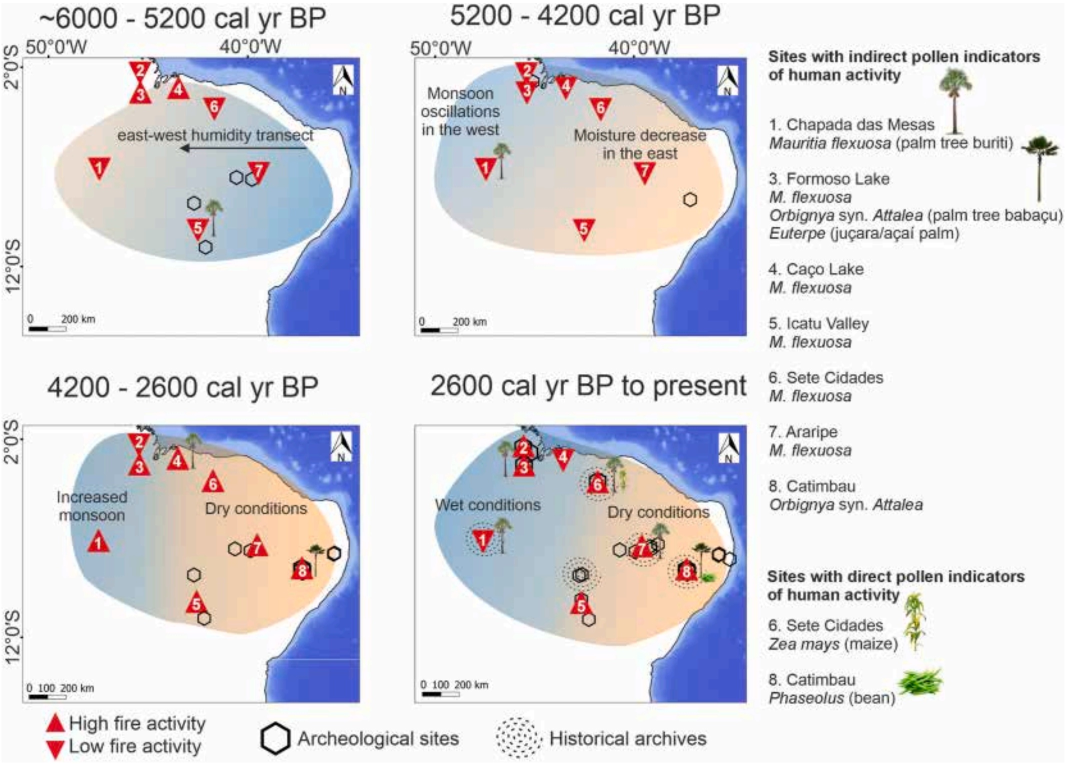

Fig. 7. 6000 years of biomass burning and human activity in NEB. Numbers refer to Fig. 2, Table 1 and Table S2. Up arrow (▲) stands for high fire activity, and down arrow (▼) for low fire activity. Sites with an anthropogenic presence are inferred from radiocarbon dates (hexagonal symbols) and historical archives (dotted spiral). Direct and indirect pollen indicators of human activity are displayed on the map, where symbols may show an offset relative to their exact location to avoid overlapping.

are most common in the Cerrado biome (Follador et al., 2023; Simon et al., 2009). Indeed, this type of fire was interpreted in the Cerrado vegetation of Lake Caço under a seasonal climate (Ledru et al., 2006). Conversely, human-induced fires result from burning both herbaceous and arboreal strata (Pivello, 2011). Most fires recorded in eastern NEB were associated with anthropogenic activity, as in Catimbau (Moraes et al., 2020), Araripe (Guerra et al., 2024; Pessenda et al., 2010), and Sete Cidades (Pessenda et al., 2010; Xavier et al., 2022). At Icatu Valley, a fire increase recorded since 4.0 ka BP (Oliveira et al., 1999) was likely of anthropogenic character given the Caatinga's lack of natural fires and any archeological signals near the site (Fig. 7). Around 3.0 ka BP, intense fires, pollen grains of *Phaseolus* (bean) and *Orbignya* (palm tree babaçu) in Catimbau were related to Amerindian practices (Moraes et al., 2020). Indeed, archeological artifacts of Tupi-Guarani traditions were observed since ~5.0 ka BP near Catimbau (Fig. 7) (Oliveira, 2006; Martin, 2013). After 450 yr BP, human occupation declined as a consequence of arid conditions and conflict with Europeans (Andrade et al., 2016). In Araripe, fires were linked first to the activity of native Kariri group, the Macro-Jê language family (Souza et al., 2020), and then to European occupation after 450 yr BP (Guerra et al., 2024). At Sete Cidades, after a period of low demographics caused by dry conditions, an increase in biomass burning observed during a wet period with pollen grains of *Zea mays* (Fig. 7) attested the presence of native groups. Land use practices intensified after 450 yr BP with the arrival of Europeans in the north of Piauí state, and anthropogenic pressures continued for 400 years until the creation of Sete Cidades National Park in 1961 (Xavier et al., 2022). Eastern NEB experienced demographic growth from 3.0 ka BP onwards during predominantly dry conditions with displacement of human settlements locally (Araujo et al., 2025). Therefore, we showed that, mostly in eastern NEB, changes in fire activity and vegetation were often related to local shifts in human activities.

During the last 2000 years, human settlements mostly related to Tupi traditions and artifacts were observed in both coastal and central regions close to water resources (Fig. 7) (Davis and Navarro, 2023; Lima-Verde, 2015; Martin, 2013; Souza et al., 2020). Tupi-Guarani land use practices included forest farming, the cultivation of maize and beans crops (Martin, 2013). After reconsideration, it is now suggested that Tupi-Guarani traditions spread from the eastern Amazon around 2.4 ka BP toward southern Brazil, occupying the Cerrado seasonally dry forests (De Almeida and Neves, 2015; Iriarte et al., 2017). So far, no dispersal modeling has been simulated for NEB. Considering the geographical extent of Tupi-Guarani culture observed across the region and the evidence of pollen records, their dispersal toward eastern NEB could date back at least to ~4.2–3.0 ka BP, a margin of 1800–600 years earlier than inferred for southern Brazil (Souza et al., 2020). In this scenario we suggest that an eastward spread of human activity was likely eased by the expansion of seasonal forest and moister forested physiognomies such as woody cerrado and palm swamps, as for instance nearby water resources at Araripe (Guerra et al., 2024) and Catimbau (Moraes et al., 2020).

In western NEB, the first record of human activity in the pollen records dates back to ~2.5 ka BP at Lake Formoso (Fig. 7) with the presence of palm trees *Mauritia*, *Euterpe*, and intense fires, related to human settlements after 1.3 ka BP (Moraes et al., 2021). At Cabeludo, pottery fragments and increased charcoal particles were recorded during this period (Moraes et al., 2022). In western NEB lowlands, stilt-house settlements and pottery have been recorded over the last millennium under wet conditions (Davis and Navarro, 2023; Navarro, 2018). In southwestern NEB, intense fires between 3.9 and 2.6 ka BP were attributed to a predominant seasonality in Chapada das Mesas, though the authors do not dismiss the hypothesis of anthropogenic fires/climate–human interactions (Xavier et al., 2024). Even considering the archeological significance of the western NEB–Amazon boundary as an ancient migration route (Goldberg et al., 2016), and the presence of *Mauritia* throughout the whole pollen record with increase and stabilization from 2.6 ka BP onward (Fig. 4c), no conclusions were drawn due to the lack of archeological charcoal datings for the Chapada das Mesas site (Fig. 7). After 3.0 ka BP, western NEB seemed less occupied by humans than the eastern NEB (Araujo et al., 2025), but this could merely reflect a lack of archeological sampling in the western inland areas compared to the eastern ones.

Over the last 500 years fire activity in most of NEB (Fig. 7) was attributed to changes in land use practices during the Brazilian colonial period. Around 1500 AC, Europeans arrived on the mainland of South America, first at the coastlands that now constitute the NEB where they began logging brazilwood trees, the earliest exploitative activity of Brazilian vegetation (Abreu, 1998; Schwartz, 1978). Then, circa 1700 AC, itinerant cattle herders started to migrate from the southeastern coast of NEB to the northern and western interior through the Caatinga and Cerrado landscapes, where they opened pastures, raised livestock, and practiced extensive deforestation (Abreu, 1998; Prado Jr, 2011). Historically, NEB was the first Brazilian territory to be occupied by Europeans (Naritomi et al., 2012), and it has undergone intensive – and chronic – disturbance since then: by 2024 it held 10 million hectares of agricultural lands (CONAB, 2024) and has suffered increasing degradation of its biomes that puts its biodiversity at peril.

Climate variability has been proposed as the main cause of demographic shifts during the MH of eastern South America (Prado et al., 2013; Riris and Arroyo-Kalin, 2019). However, the radiocarbon dates compiled in our study (Table S4) indicate that human populations were present during both NEB's wet and dry phases over the last 6000 years, and persisted under the predominant dry climate (Fig. 7). It has been suggested that reoccupation of areas in eastern NEB with favorable local conditions would have allowed human groups to survive (Araujo et al., 2025). Therefore, NEB's anthropogenic activities were not directly responding to the east–west humidity gradient, but instead would be a result of adaptive strategies to environmental conditions relying on natural resources available in each biome of the region (Martin, 2013).

6. Implications for biodiversity conservation

Our study highlights how the distribution of vegetation throughout NEB during the last 6000 years was influenced by both ITCZ and SAMS shifts. We show that human activities in both the Cerrado and Caatinga were more conditioned to the availability of environmental resources and adaptation efficiency than to the humidity gradient. This is crucial to fully understanding the impact of ongoing global warming on both biodiversity and ecological processes in the Brazilian semi-arid regions at centennial and millennial scales. Significant changes in the distribution of the vegetation were observed around 5.2 ka BP with the westward expansion of the Amazon rainforest and Cerrado, and after 4.2 ka BP with the eastern expansion of the Caatinga. Two refugia, the moist forest at Maranguape and the cerrado at Araripe, were fully developed after 2.6 ka. However, our framework shows that the regional vegetation (e.g. montane moist forest, dry forest caatinga, and woody cerrado), from east to west, was particularly sensitive to severe drought episodes at short- and long-terms (Fig. 4c). Moreover, the woody cerrado as in Chapada das Mesas and montane forest in Maranguape showed a recovery time of more than 100 years (Fig. 4c), with a shift in the vegetational composition dominated by drought-related taxa and more open physiognomies (Montade et al., 2014; Xavier et al., 2024). This is different to the Cerrado of central Brazil, where the vegetation recovery took about 30 years after drought or intense biomass burnings (Escobar-Torrez et al., 2023). Human-induced fires and land use activities over the last 3000 years were practiced regardless of climate conditions all over NEB although with no impacts on vegetation composition. From 1500 AD onward, changes in human practices influenced the composition of plant communities (Moraes et al., 2020; Xavier et al., 2022). Today, conservation policy in NEB is covered by the New Brazilian Forest Code (Law N°. 12651/2012) that regulates Permanent Protected Areas (PPAs), Legal Reserves (LRs), and Indigenous Lands (ILs) for biodiversity protection and sustainable use of natural resources, and defines the proportions of land use and native vegetation within rural properties (Brancalion et al., 2016). Thus, we infer that these current policies will not be effective in maintaining the region's biodiversity on both short- and long-term scales: the spatiotemporal limitations of PPAs and LRs do not consider biodiversity redistributions, vegetation shifts, and biome fragmentation caused by human pressures and climate changes.

Given the accentuated degradation processes afflicting NEB landscapes, a need for updating conservation policy was evidenced (Silva et al., 2023). Since the species composition and human practices change across the region, specific protection laws and land use regulations are required to properly manage and conserve each biome. Recently, an environmental assessment for NEB (Vieira et al., 2021) pointed out that changes in land management are one of the main drivers of desertification through the loss of native vegetation. Changes of geographical limits, biased distributed reserves, and the lack of ecotone delimiting (e.g. Cerrado enclaves on Amazonia and Caatinga) affects land use regulations and restricts the efficacy of conservation laws (Vieira et al., 2022). In NEB, a study carried out in a Cerrado–Caatinga ecotone showed that PPAs reduce the probability of deforestation (de Espindola et al., 2021). A recent phytosociological survey in Caatinga (Macêdo et al., 2024) concluded that human-degraded areas still retain the potential for natural regeneration, the authors arguing that the creation of new interconnected conservation units through LRs, vegetation remnants, and PPAs may help to maintain biodiversity. However, when we take into account that PPAs are spatiotemporally limited, such an approach may be ineffective in safeguarding species and confronting global change scenarios (Velazco et al., 2019). Today, only 14.41 % of Cerrado is protected in PPAs (Vieira et al., 2022), and less than 8 % of the Caatinga is legally protected under current legislation, with only 1.3 % in LRs (Teixeira et al., 2021). In NEB, 25 % of the original Amazon Forest is in conservation units and ILs (Celentano et al., 2017), but nevertheless the forest is still highly fragmented due to the loose implementation of the Forest Code (Silva-Junior et al., 2022). For the Atlantic Forests of NEB, less than 4 % of its 13 % remaining cover is under protection (Ribeiro et al., 2009).

In this rather bleak context, we suggest that the creation of flexible networks that combine the inclusion of dynamic conservation areas with PPAs (D'Aloia et al., 2019) could be a priority for conservation effectiveness in NEB. For effective conservation at decadal, centennial, and millennial timescales, including facing the ongoing climate crisis, it is necessary for each conservation unit, individually, to contemplate spatial and abiotic gradients (climate and soil) (Marengo et al., 2020; Marengo and Bernasconi, 2015). These gradient units must occur within and between biomes considering ancient (Ledru and de Araújo, 2023) and future climatic corridors of biodiversity. These flexible models would ensure vegetation recovery and follow biodiversity redistributions, as about 59 % of documented species range shifts are correlated to climate changes (Lawlor et al., 2024). Moreover, the integration of flexible models with ecological connectivity could increase the long-term probability of species' persistence and the retention of ecosystems processes (Beger et al., 2022) in the region. Such an approach could be useful in the following scenarios: to promote restoration of Caatinga's anthropically altered and fragmented landscapes (Antongiovanni et al., 2020; Macêdo et al., 2024) and to mitigate the Cerrado's biodiversity and ecosystem losses. These are currently facing an even graver threat in the shape of the MATOPIBA expansion, the latest emerging Brazilian agricultural frontier (Silva, 2020) located in the Cerrado–Caatinga ecotone, concurrently the largest burned areas within the entire biome (Argibay et al., 2020; Martins et al., 2024).

7. Conclusion

Changes in vegetation over the last 6000 years tracked back the position and intensity of an east–west precipitation gradient established by the climate models and speleothem records, although with some differences between coastal and inland regions. Our results highlight a strong spatial variability of the South America monsoon and convergence zones over NEB, thus delimiting the specific location of the moisture band from its associated patterns of vegetation change. From 6.0 to 5.2 ka BP, open landscapes prevailed under lower-than-today rainfall in the west, while woody cerrado and mangrove were observed on the coast. Then, from 5.2 to 4.2 ka BP, humid forests expanded across most of NEB under higher-than-today rainfall, while a dry-adapted open vegetation was still observed in the eastern inland region. Local variations in soil moisture due to sea level rise at 6.0 ka BP in western NEB and oscillating rainfall patterns after 5.2 ka BP in eastern NEB drove the aforementioned differences in sites located out of the moisture band. After 4.2 ka BP, woody cerrado and rainforest became established in the west under increased moisture, whereas the xerophytic Caatinga prevailed in the east under dry conditions. These changes are in agreement with the seesaw precipitation behavior that split the NEB into two climatic subregions circa 4.2 ka BP, when the west (east) became wetter (drier) than before, due to a stronger monsoon convection and ITCZ spatial variability in response to tropical Atlantic SSTs, as documented by TraCE-21k simulations. Moreover, we showed that the 4.2 ka dryness event in NEB affected the regional vegetation under short and long rainy seasons. Western Cerrado and eastern montane forests were vulnerable to extreme dryness, with reorganization of biodiversity and a recovery time exceeding one century. Fires were not very frequent over most of the region until 4.0 ka BP, when an increase in fires often linked to anthropogenic activity was recorded during both wet and dry periods across NEB.

Our data set provides a solid framework for both short- (decadal) and long-term (centennial to millennial) timescales. Future studies focusing on transitional climatic areas would allow us to improve our knowledge of NEB climate–vegetation boundaries during the Holocene. The ongoing climate change that we are witnessing in the 21st century will exacerbate the pressure on resources, and changes in land use practices should be defined in light of better knowledge of the past to promote sustainable economic development in the future. Those actions will be crucial if we are to guarantee the effectiveness of conservation policy and new land use regulations in such a vast and socio-environmentally diverse region.

Credit authorship contribution statement

Sergio Augusto Santos Xavier: Conceptualization; Data curation; Investigation; Methodology; Formal analysis; Visualization; Writing – original draft; Writing – review and editing. Marie-Pierre Ledru: Conceptualization; Data curation; Funding acquisition; Investigation; Methodology; Project administration; Resources; Supervision; Visualization; Writing – review and editing. Ilana Wainer: Validation; Writing – review and editing. Myriam Khodri: Validation; Writing – review and editing. Francisca Soares de Araújo: Funding acquisition; Investigation; Project administration; Resources; Supervision; Validation; Writing – review and editing.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.quascirev.2025.109723.

Data availability

All data and/or code is contained within the submission.

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