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Palaeoenvironments in semi-arid northeastern Brazil inferred from high precision mass spectrometric speleothem and travertine ages and the dynamics of South American rainforests

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Introduction

Understanding past environmental changes in tropical rainforests is extremely important in order to assess the response of such environments to present and future climatic changes and understand causes and the present patterns of biodiversity.

Earlier hypothesis on the origin of biodiversity have stressed the role of past climatic changes in promoting speciation. According to the "refuge hypothesis" (Haffer, 1982), dry periods could have led to forest fragmentation, isolating more humid forested zones (called refuges) within an environment largely dominated by savannas. The refuge hypothesis does not assign timescales for rainforest fragmentation, although recent studies have suggested that speciation could have occurred over timescales of millions of years (Knapp and Mallet, 2003). Although the focus of heavy criticism (Colinvaux, *et a.*, 2000), the refuge hypothesis has generated a large amount of research. In general, pollen studies (Colinvaux, *et al.*, 1996, Haberle and Maslin, 1999) tend to support a continuous forest cover throughout late Quaternary climatic shifts, although large variations in rainfall have also been demonstrated by other pollen and isotopic studies (van der Hammen and Absy, 1994; Maslin and Burns, 2000).

Amazon and Atlantic rainforests are the two major forested zones in South America. Amazon rainforest, the largest rainforest in the world, comprise a total original area of 4.1 million km^2 and is renowned for hosting the large biodiversity in the world (30% of all the world's known plant and animal species). Atlantic rainforest, also a biodiversity hotspot, occurs along the coast and has been subjected to heavy deforestation since European arrival. Nowadays only c. 7% of its original forested area of 1.3 million km^2 remains. These two rainforests are separated by drought-prone semi-arid northeastern (NE) Brazil. Our study does not address the refuge hypothesis directly although it sheds new light on the dynamics of forest expansion in the past as well as indicates alternative ways of promoting speciation. It has long been hypothesized, due to botanical (Mori,

1989; Andrade-Lima, 1982) and faunistic (Costa, 2003) similarities, that the Amazon and Atlantic rainforests were once linked in the past. Although numerous connecting routes have been postulated (Bigarella, *et al*, 1975; Por, 1992; De Oliveira, *et al*, 1999), the timing of forest expansion and their possible recurrence have remained elusive.

The study area lies in the driest portion of NE Brazil "dry corridor", close to the village of Laje dos Negros, northern state of Bahia. Mean annual precipitation is around 480 mm and potential evapotranspiration is in excess of 1,400 mm/year (Fig.1). Present vegetation comprises a low arbustive scrubland known locally as caatinga. The area contains a well-developed underground karst (Auler and Smart, 2003) with abundant secondary calcite precipitates, both underground (speleothems) and on the surface (travertines).

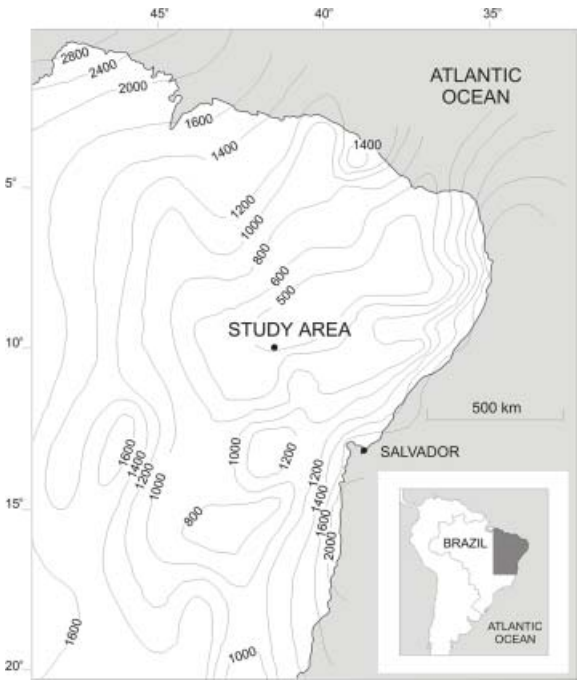

Fig.1. Location of the study area.

Here we examine shifts in the boundaries of both Amazon and Atlantic rainforest through systematic analysis of past pluvial (and thus forested) periods in NE Brazil. ^{230}Th analyses of calcite speleothems and surface travertines were used to constrain wetter than present intervals. Palaeobotanical analyses of fossil flora embedded in dated travertine allowed plant identification and floristic reconstruction.

Past pluvial periods

Fifty-four ^{230}Th ages of growth phases in 11 speleothems and fifty-five travertines samples were obtained with thermal ionisation and inductively coupled plasma mass spectroscopic techniques. Because of the net deficit between rainfall and evapotranspiration there is no speleothem or travertine deposition at present. Thus, any ages unequivocally indicates wetter than present conditions.

Top and bottom ages of speleothems indicate that NE Brazil pluvial phases were short and widely spaced. Because there is an infiltration threshold to be overcome in order to generate speleothems, the speleothem record should be interpreted in terms of pluvial maxima. Major speleothem growth phases occur at 14,800 – 15,900, c. 39,000, c. 48,200, c. 60,200, c. 73,000, c. 86,500, c. 110,000, c. 136,000, c. 179,000 and c. 207,500 yr B.P. These growth intervals coincide precisely with Heinrich events and stadials in the Northern Hemisphere. Travertine data complements the speleothem record, including times not wet enough to generate speleothems. Younger Dryas and Last Glacial Maximum ages are represented, as well as very old (0.9 Ma) ages based on initial δ^{234}U of younger nearby travertines. The last phase of travertine deposition in several sites yielded concordant ages around 11,700 yr B.P., indicating that NE Brazil became too dry to promote calcite precipitation after that. Travertine ages, besides indicating moister conditions, help constrain the age of the abundant botanical fossil remains embedded in the calcite matrix.

Further ^{230}Th and radiocarbon analyses were performed respectively in calcite samples associated with fossil bones of vertebrates and in fossil bat guano, attempting to bracket the age of fossil emplacement and help reconstruct NE Brazil palaeoenvironments.

Forest expansion and ecological changes

Travertines present abundant botanical fossil remains, including well-preserved trunk, root and leaf casts. Ongoing systematic leaf identification has allowed the description of 45 morphological types. Although present caatinga vegetation shows predominance of coriaceous leaves, the large majority of fossil leaves are membraneous (less than 5% of coriaceous

leaves in most sites). Fossil leaf area larger than caatinga species suggests low luminosity and thus closed forested conditions. Brochidodromous venation (common in the Atlantic rainforest but nearly absent in the caatinga) comprises a significant portion of the deposits. Furthermore, the absence of Melastomataceae in the analysed samples suggests a stabilised forest ecosystem (Rizzini, 1997).

Overall, the palaeoflora of the travertine deposits indicate a mesophilic semi-deciduous forest typical of more humid environments, nowadays found only in isolated relict forested zones known as brejos. The assemblage of fossil plant species suggests the expansion, during the wet phases of the Quaternary, of a dense forest that replaced, or mixed with, the caatinga vegetation. Due to the widespread occurrence of travertine deposits with similar palaeobotanical association in NE Brazil, forest expansion appears to have been a regional phenomenon, providing a possible connection route between the Atlantic and Amazon rainforests.

Fossil mammal remains have also been frequently found within caves in NE Brazil, sometimes covered with a thin veneer or calcite. Although ^{230}Th analyses have been performed in several calcite coatings, assigning precise ages to the fossils themselves is difficult due to the unknown time lag between fossil death at the surface, emplacement into the cave and later calcite precipitation. Furthermore, the fossil emplacement mechanism causes bias in the fossil record and thus cave fossil assemblages rarely mirror fauna at the surface. Due to these limitations it is risky to interpret palaeoenvironments based solely on the mode of living of cave fossil assemblages. Nevertheless, former habitats of individual species can yield useful information on past environmental conditions, although many fossilised remains in NE Brazil belong to ecologically versatile species belonging to genus Puma (living Jaguar) and Mazama (living deer).

Habitats of some of the fossil species probably differed markedly from the now semi-arid and vegetation-poor scenery of NE Brazil. Fossils of llama and extinct bear probably indicate a cooler environment because closest living relatives now live in much colder environments. Because all living monkeys in the New World are arboreal, the two fossil species of giant monkeys (Hartwig and Cartelle, 1996; Cartelle and Hartwig, 1996) are likely to suggest a more forested environment. Local caves are nearly devoid of bat colonies at present, although there is massive guano and fossil bat bone accumulations. Some of the twenty species identified by Czaplewski and Cartelle (1998) now occur only in rainforest biomes, suggesting a moister and more forested environment at time of bat occupation. Three radiocarbon analyses on bat remains have yielded calibrated ages of c. 20,000, c. 23,000 and > 44,000 yr B.P. Overall, vertebrate fossil species data conforms with palaeobotanical data, suggesting past episodes of moister and more forested environments.

Final considerations

Dry NE Brazil, bridged inbetween the Amazon and the Atlantic rainforests, is regarded as a major impediment for the present migration of floral and faunal specimens between both rainforests. Numerous studies, however, have pointed out at similarities between Atlantic and Amazon fauna and flora. Caatinga vegetation shows some intriguing similarities with Amazonia vegetation (Prado and Gibbs, 1993) and late Pleistocene pollen data from a NE Brazil site contains taxa nowadays restricted to the Amazonian and Atlantic rainforests (De Oliveira, *et al*, 1999). Our study has constrained the timing of several Pleistocene pluvial periods associated with forest expansion in NE Brazil. These more humid intervals have caused significant boundary shifts in South America's major rainforest, creating forested routes through NE Brazil. Such periodic forested links were responsible for promoting major biotic interchange, favouring faunal and floral species migration and speciation.

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