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Stability of a Neotropical microrefugium during climatic instability

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ABSTRACT

Aim The primary objectives of this study were (1) to assess, in the light of palaeoecological reconstruction, the climate stability hypothesis used by evolutionary biologists to explain high diversity in historically stable areas, and (2) to identify the response mechanisms of a tropical rain forest microrefugium to climatic variability.

Location North-eastern Brazil, Serra de Maranguape.

Methods Vegetation and climatic changes were reconstructed using a pollen record in a sediment core from a forest hollow, and the chronology was based on accelerator mass spectrometry radiocarbon analyses.

Results Past vegetation dynamics consisted of three main forest types, shown by major compositional changes in rain forest assemblages between 5000 and 1000 cal. yr BP. Dense ombrophilous forest was abruptly replaced by heliophilous early successional tree taxa at 4275 cal. yr BP. These early successional tree taxa were established over a period of *c.* 100 years, and their dominance lasted for *c.* 750 years and was associated with dry conditions until 3525 cal. yr BP. Subsequently, the expansion of secondary successional tree taxa over a period of *c.* 550 years enabled the recovery of ombrophilous forest.

Main conclusions The vegetation changes in the Serra de Maranguape provide evidence for the high sensitivity of this rain forest microrefugium to climatic variability on a multidecadal to millennial time-scale during the mid- to late Holocene. Despite the substantial compositional and climatic changes, this microrefugium apparently was continuously forested and responded to climatic instability by recruiting key species to its highly diverse stock. This evidence helps to address the joint concerns of evolutionary biologists and palaeoecologists regarding how forests can persist during periods of climatic variability by showing that some tropical regions can remain continuously forested despite reorganization during abrupt and short-term climatic changes.

Keywords
Climate change, diversity, historically stable area, Holocene, microrefugia, north-eastern Brazil, palaeoecology, pollen analysis, rain forest.

INTRODUCTION

The Quaternary covers the past 2.6 million years and has been characterized by changes in the Earth's orbital geome- and diversification (Hewitt, 2000; Parmesan & Yohe, 2003). In tropical South America, climatic changes involved a specific combination of climatic variables that have been shown to influence species life history (e.g. Haffer, 1969; Costa,

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studies have been combined with palaeohabitat simulations and used to reconstruct landscape dynamics spatially across the Quaternary (Carnaval & Moritz, 2008; Werneck *et al.*, 2011, 2012). These simulations have shown that high contemporary species diversity is associated with historically stable areas or 'refugia'. In contrast to climatically unstable areas, where the forest is subject to phases of fragmentation and expansion in response to extreme climatic changes, historically stable areas are associated with climatic stability on geological time-scales (Carnaval & Moritz, 2008). However, as palaeoenvironmental analyses in historically stable areas are rare in the tropics, little is known about the past behaviour of plant communities when they are restricted to such areas.

Today, historically stable areas can correspond to small areas characterized by vegetation that is very different from that of the broad landscape, and in which the vegetation is isolated from the rest of its natural range. In north-eastern Brazil (hereafter referred to as 'Nordeste'), the tropical rain forest has this pattern of distribution. The Amazonian and Atlantic rain forests grow in the north-western and eastern coastal areas, respectively, while scattered 'pockets' of rain forest can be found in mountainous areas in the northern Nordeste surrounded by the semi-arid vegetation that covers the lowlands. Palaeoenvironmental records from the northern Nordeste reveal lowland expansion of the tropical rain forest in this subregion that lasted for 4000 years during the last deglaciation (Behling *et al.*, 2000; Ledru *et al.*, 2002, 2006, 2007). Then, at the beginning of the Holocene, the tropical rain forest was replaced by either savanna (Cerrado) or xeric shrubland (Caatinga). Despite the expansion of drier biomes in lowland areas, today, the tropical rain forest persists in some humid mountainous areas of the northern Nordeste. These forests thus appear to have survived in the most arid region of Brazil throughout the Holocene and can be considered as relicts of the expansion of lowland rain forest during the last deglaciation. In addition, the present-day composition of the forest in these mountainous areas is characterized by specific species of both Amazonian and Atlantic forests, highlighting their past connection with the lowlands (Andrade-Lima, 1982). Consequently these 'pockets' of tropical rain forest can be considered as 'microrefugia', namely small populations that survive outside their main area of distribution because they are protected from unfavourable regional environmental conditions (*sensu* Rull, 2009). High-resolution palaeoclimatic analyses of the Nordeste during the Holocene, however, show that in fact the climate was not stable and that changes occurred on various time-scales (Cruz *et al.*, 2009). Consequently, it might be expected that such microrefugia in the Nordeste were not completely 'stable' but were subject to decadal and multidecadal changes in precipitation.

The aim of our research is to document changes in key plant communities that responded to climatic variability cally and ecologically stable over millennia. The question whether short-term climatic changes have consequences for the reorganization of plant communities within microrefugia and for species richness has not yet been widely explored. To this end, we collected a sediment core in the humid mountainous area known as the Serra de Maranguape that corresponds to a microrefugium of tropical rain forest and that can be considered as an example of a historically stable area.

MATERIALS AND METHODS

Study area

The Serra de Maranguape is a mountainous area reaching 920 m a.s.l. (3°53′40.32″ S, 38°43′13.56″ W), located 30 km from the Atlantic Ocean in the state of Ceará in the Nordeste (Fig. 1a). The Nordeste is characterized by a humid to sub-humid climate in the eastern and north-western coastal areas, while its central area is characterized by a semi-arid climate that corresponds to the driest area of Brazil, called the Sertão. In this subregion, the annual precipitation of between 500 and 1500 mm is exceeded by annual potential evapotranspiration of between 2000 and 3000 mm, causing a serious water deficit. Despite the dry conditions in the lowlands, a sub-humid climate persists in mountainous areas of the northern Nordeste. As show by data from Guaramiranga (830 m a.s.l.), located in the Serra de Baturité just 50 km south of the Serra de Maranguape (Fig. 1b), the mean annual precipitation is higher than in the lowlands (Fig. 1c). The incidence of rainfall is influenced by elevation: at higher elevations the air is cooled, causing frequent fogs and high orographic precipitation, which is higher on the windward side and lower on the leeward side. In addition, rainfall under the influence of the Atlantic Ocean decreases rapidly with distance from the coast (e.g. Uvo *et al.*, 1998), as observed inland at Quixada (Fig. 1c).

In the northern Nordeste, precipitation seasonality is strongly influenced by the natural migration of the Intertropical Convergence Zone (ITCZ), which is itself controlled by the seasonal differences in the sea-surface temperatures between the two hemispheres (Hastenrath, 1991). Characterized by maximum cloudiness and precipitation, the ITCZ shifts southwards during the wet season above the northern Nordeste, while during the dry season the ITCZ is located to the north. Even though most precipitation occurs between February and March, the dry season in mountainous areas is mitigated by the decrease in evapotranspiration and frequent fogs (Fig. 1c). However, interannual variability of precipitation is high in this region and is generally caused by a significant change in the position of the ITCZ, leading to either severe droughts or floods (Fig. 1c). These dramatic events are often associated with large-scale climatic phenomena, such as the El Niño–Southern Oscillation or the meridional

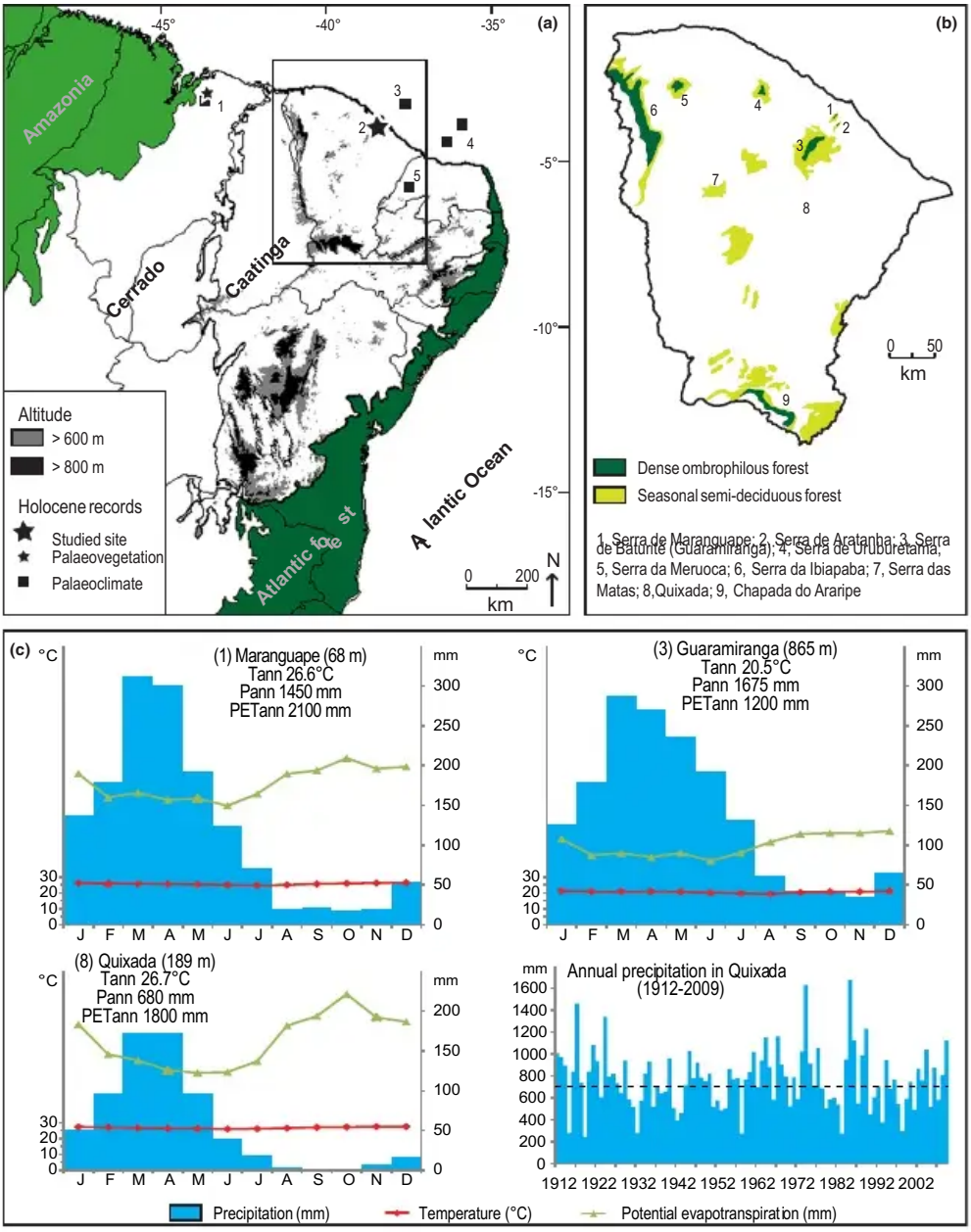

Figure 1 (a) Study site, with the distribution of the various biomes in north-eastern Brazil drawn by DIVA-GIS software. The mountainous areas plotted in the Caatinga biome show the main areas in which tropical rain forests grow. Stars and squares show the locations of other Holocene palaeovegetation and palaeoclimatic records, respectively: 1, Ledru *et al.* (2002, 2006), Sifeddine *et al.* (2003), Jacob *et al.* (2004), Pessenda *et al.* (2005); 2, this study; 3, Arz *et al.* (1998); 4, Arz *et al.* (1998, 2001), Jaeschke *et al.* (2007); 5, Cruz *et al.* (2009). (b) State of Ceará, showing the distribution of tropical rain forest in relation to the distribution of mountainous areas, including the locations discussed in the text. (c) Climate seasonality of northern Ceará, illustrated by three ombrothermic diagrams (data were retrieved using NEW_LOCCLIM software; Grieser *et al.*, 2006) and one diagram of historical precipitation (data were retrieved from the Fundação Cearense de Meteorologia e Recursos Hídricos, available at: http://www.funceme.br/). The ombrothermic diagrams show monthly mean of temperature, precipitation and potential evapotranspiration and specify mean annual temperature (Tann), mean annual precipitation (Pann) and mean annual potential evapotranspiration (PETann). The diagram of historical precipitation data represents interannual variability of precipitation over the last century in Quixada; the dashed line represents mean annual precipitation.