Quaternary Science Reviews 122 (2015) 158–165

Contents lists available at ScienceDirect

Quaternary Science Reviews

journal homepage: www.elsevier.com/locate/quascirev

New insights on palaeofires and savannisation in northern South America

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ARTICLE INFO

Article history:
Received 17 March 2015
Received in revised form
28 May 2015
Accepted 29 May 2015
Available online

Keywords:
Savannas
Rainforests
Savannisation
Fire
Neotropics
South American settlers
Conservation
Younger Dryas

ABSTRACT

Understanding the origin and ecological dynamics of tropical savannas in terms of natural and human drivers of change is a hot topic that may be crucial for conservation. The case of the Gran Sabana (GS), a huge savanna island within the Amazon-Orinoco rainforests, is presented as a pilot study for the Neotropics. A vivid debate exists on whether or not forests formerly covered the GS and on the potential role of anthropogenic fires in the establishment of present-day savannas. This debate has generated a conflict between conservation ecologists defending the ancient forests hypothesis and indigenous inhabitants (Pemones), for whom the use of fire is an inalienable cultural trait. Here we discuss the latest palaeoecological findings documenting past vegetation dynamics and the shaping of present GS landscapes. At the beginning of the Younger Dryas (YD), the GS was more forested than it is today but an abrupt, hitherto irreversible, shift toward savannisation, likely caused by coupled climate-fire synergies, was recorded between the mid-YD and the Early Holocene. It is suggested that fires could have been ignited by the first South American settlers in their eastward migration from the Panama Isthmus through the so called Atlantic Route. The Pemones would have established in the GS during the Late Holocene when savannas already covered the region. A simplistic debate between either forest or savanna as the "original" GS vegetation is unrealistic and should be replaced by a more dynamic approach. The term "original" vegetation itself is misleading and should not be used.

1. Introduction

Savannas cover approximately 20% of the global land surface and are especially widespread across the tropics and subtropics (Woodward et al., 2004). A variety of climatic, edaphic and human drivers have been invoked to explain the origin and persistence of tropical savannas, but climate-fire interaction has been considered a major cause of the current and historical savanna expansion (Jacobs et al., 1999; Beerling and Osborne, 2006). At present, the influence of human fires on most tropical savannas is manifest and has been used as support for a potential anthropogenic origin of many of these grassy communities. However, empirical evidence for this and other hypotheses should be based on long-term studies, preferably based on palaeoecological evidence (Rull and Vegas-Vilarrúbia, 2011).

In this paper, we analyse the case of the Gran Sabana (GS) as a pilot survey for the Neotropics. The GS region, which is located in SE Venezuela, is part of a huge savanna island of ~68,000 km^2, known as the Roraima Savannas, which lies within the extensive Amazon-Orinoco rainforests (Barbosa and Campos, 2011) (Fig. 1). The occurrence of these savannas has been considered by some an anomaly because the regional climate is more suitable for the surrounding rainforests. Therefore, a potential anthropic origin for these open grassy communities is implicit or explicit in many studies. Other hypotheses consider these savannas a relic of former drier (glacial) climates or the natural consequence of edaphic and climatic conditions (reviewed in Montoya and Rull, 2011). Most of the GS is covered by treeless savannas dominated by C_4 grasses (notably *Axonopus* and *Trachypogon*), with forest–savanna mosaics at the edges and gallery forests along rivers (Fig. 2). The "morichales", palm swamps dominated by *Mauritia flexuosa*, are emblematic and widespread in the southern sector of the GS, roughly below 1000 m elevation (Rull, 1998; Rull and Montoya, 2014). The GS region is under protection by several entities

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http://dx.doi.org/10.1016/j.quascirev.2015.05.032
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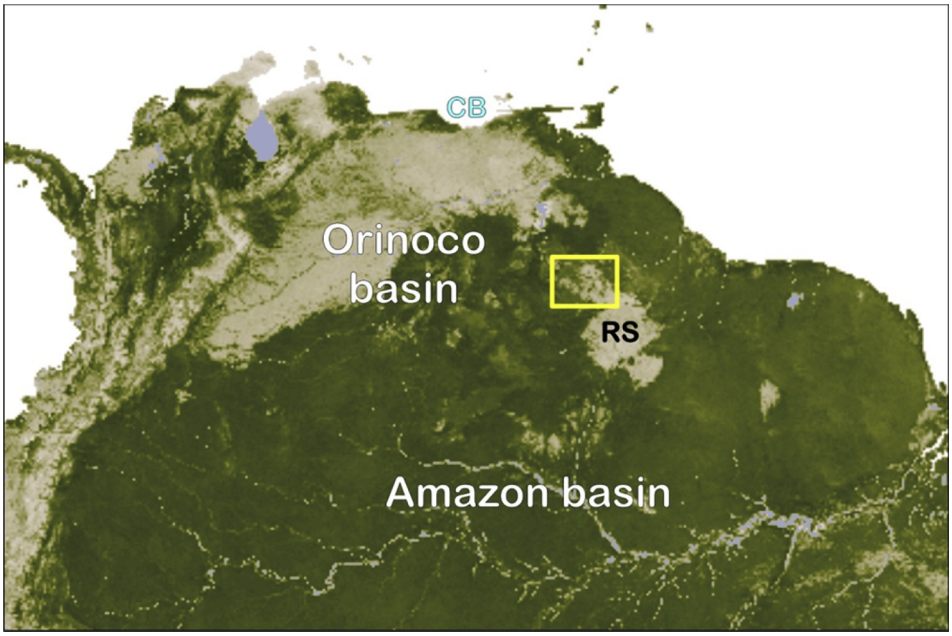

Fig. 1. Map of northern South America showing the general distribution of forests (green area), based on MODIS leaf area index. The Gran Sabana region is indicated by a yellow box. CB – Cariaco Basin, RS – Roraima Savannas. Base map: NASA Earth Observatory, downloaded from http://earthobservatory.nasa.gov/IOTD/view.php?id=7705 (26 Feb 2015). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

including a National Park, a Biosphere Reserve and a World Heritage site (Huber, 1995a,b). The region is in the headwaters of the Caroní river, a tributary of the Orinoco that has been intensively exploited for hydroelectric power by the state company Corpoelec (formerly EDELCA) for several decades (Castro and Gorzula, 1986).

At present, the GS savannas are in expansion, to the detriment of forests due to the frequent burning by indigenous people of the Pemón culture (Kingsbury, 2001; Rull et al., 2013). This has fostered an intense debate between defenders and detractors of these practices. Defenders of the Pemón practices argue that fire management is a fundamental part of the traditions of this indigenous group and that it should be preserved not only for cultural reasons but also because of its potential usefulness for conservation. These scholars postulate that the GS savannas have dominated the region for thousands of years and are the "natural" GS landscape in which the Pemón lifestyle developed. On the contrary, the critics of indigenous fire practices -championed by EDELCA, which has a special fire department and sponsors extensive firefighting campaigns to protect the Caroní headwaters- believe that fires have been responsible for the disappearance of the hypothetical ancient forests that covered the GS before the onset of human fire practices (Dezzeo et al., 2004b; Rodríguez, 2004). This debate is relevant in terms of conservation, as the detractors of the Pemón practices argue that forest clearance should cease at once and that fire should thereafter be firmly combatted; whereas the Pemón defenders believe that their traditional knowledge, including the use of fire, is useful for proper land management and that it should be included in conservation planning (Sletto and Rodríguez, 2013). This controversy places the issue in a wider context as part of an ongoing discussion of global scope concerning the potential role of indigenous cultures in conservation management, especially in conflicting situations involving protection rules on areas owned by indigenous groups, as is the case of the GS (e.g. Schmidt and Petterson, 2009; Rutte, 2011; Middleton, 2013).

This paper updates and reviews the available palaeoecological evidence so as to contribute to our knowledge of the history of GS vegetation, the savannisation trends in this region and their possible environmental and human drivers. The results of this analysis are placed in a regional neotropical context and the resulting patterns are used to evaluate the potential relationship of these trends to the initial peopling of northern South America. It should be stressed that most of the GS palaeoecological records available so far correspond to the southern sector, which differs from the northern sector in several topographic, climatic and biotic aspects. Palaeoecological studies from the northern sector are in progress and will hopefully provide a more representative picture of the GS as a whole.

2. Holocene savannas

Most GS palaeoecological records are restricted to the Holocene. The first records showed that treeless savannas have been dominant at least since the Middle Holocene (Rull, 1992, 1999). Further records extended the temporal window to the Early Holocene and led to the same conclusion (Montoya et al., 2009); thus the evidence remains inconclusive with respect to whether forest or savanna constituted the "original" GS vegetation (Rull, 2009a). Some records show phases of local forest expansion – at that time the forests were dominated by Moraceae and other Urticales- around lakes and rivers during the Middle Holocene with further reductions during the Late Holocene (Ballesteros et al., 2014). The first significant vegetation shift relevant to the forest–savanna debate was found in the Mapaurí peat bog, where *Catostemma* (Malvaceae) forests were replaced by treeless savannas at ~10,200–9800 cal y BP (Table 1) (Supplementary data). This vegetation shift has been attributed to the interplay between climate and fire (Rull, 2007, 2009b). The main handicap in Mapaurí was dating. Indeed, one single radiocarbon date was obtained for this sequence (Table 1), making impossible to establish a reliable age-depth model. However, the date obtained almost exactly matched the forest–savanna replacement; therefore, the estimated age for this significant vegetation change can be considered reliable. A general corollary of this section is that savannas have