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Holocene Paleoecology in the Neotropical Savannas of Northern South America (Llanos of the Orinoquia Ecoregion, Colombia and Venezuela): What Do We Know and on What Should We Focus in the Future?

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We provide an overview of the Holocene paleoecology of the Llanos ecoregion. A region that captured the attention of researchers for more than 200 years, as it exhibits a high heterogeneity in landscapes and vegetation, where savanna and forest mosaics exist. Located in an area influenced by the seasonal migration of the Intertropical Convergence Zone (ITCZ), it provides a unique area for understanding long-term dynamics of climate, vegetation and human history. Twelve locations have been paleoecologically studied, showing general vegetation and climate changes trends since the Last Glacial Maximum (LGM). During LGM savanna herbs were dominant, indicating dry climatic conditions. The transition of the Holocene was characterized by a slight increase in forest taxa, suggesting a transition to a wetter climate. Between ∼10,000 and 7,000 cal yr BP, grasslands were abundant, and few forest taxa, including *Mauritia* were also common but rare, pointing to a warm and humid climate. After ∼7,000 cal yr BP, the gallery forest started to expand, suggesting a change to a wetter climate. *Mauritia* palms increased markedly after 4,000–3,000 cal yr BP, possibly driven by higher mean annual precipitation and/or longer wet season. The start of human occupation remains unclear, but it has been linked to the time of expansion of *Mauritia*, a period in which fires, possibly of anthropogenic origin, were more frequent. To understand patterns of change in these ecosystems, it is necessary to improve the chronological control of the sediments in future studies and increase the resolution and proxies used to reconstruct their history.

Keywords: neotropics, Colombia, Venezuela, Orinoquia, Palynology, gallery forests, savannas

INTRODUCTION

The Llanos Orientales in Colombia and the Orinoco Llanos in Venezuela, known as the Llanos of the Orinoquia ecoregion, represent the second-largest Neotropical savanna ecosystem covering more than 500,000 km^2 with an extension of about 1,200 km. The savanna starts at the foothills of the Colombian Oriental Andes extends along the Orinoco River to the swampy forest and wetlands of eastern Venezuela, almost to its delta (Berrio et al., 2002). In general, two well-defined landscapes exist the high llanos (locally known as *llanos arriba*), reaching 300 m asl, and the low llanos (*llanos abajo*) (Gassón, 2002), while the natural vegetation can be summarized in four types: forest, dry savannas, wet savannas, and swamps (**Figure 1**; Etter, 1998; Rangel-Ch, 2019). These ecosystems harbor a high ecological diversity and provide different services for the local fauna and human populations. Surprisingly the Llanos region has received little conservation attention compared to the Amazonian or Andean adjacent ecosystems (Romero-Ruiz, 2011), with just 5% of its area protected or monitored as part of conservation units. Since the 1980s, the establishment of large-scale intensive agriculture (palm oil—*Elaeis guineensis* and rice) and increased human population have modified the natural savannas and forest of the Llanos Orientales. Other activities such as cattle expansion, road infrastructure, petroleum activities, mining and illicit crops have contributed to land degradation and turned it into one of the most threatened ecosystems in Colombia (Romero-Ruiz et al., 2012).

The ecoregion is characterized as one of the main areas of wetlands distribution of the Orinoco basin, containing 38 of the 49 types of natural wetlands recognized (Lasso et al., 2014). Climate change is directly impacting wetlands through net loss of wetland areas within sites due to drying (Xi et al., 2021), desertification, erosion, biodiversity loss and ecosystem services (Convention on Wetlands et al., 2021). The lowlands of the Llanos, due to their location, are influenced by the seasonal migration of the Intertropical Convergence Zone (ITCZ), whose variations in amplitude and form seem to be one reason for major climate changes since Holocene times in the Amazon Basin and its surroundings (Behling and Hooghiemstra, 2000; Wille et al., 2003; Jaramillo-J et al., 2019a,b; Minorta-Cely et al., 2019). On the multiple factors (fire, soil types, micro-relief, hydrological regime and human activities) that limit forest expansion to the savannas, fire (natural or anthropogenic) appears to be the most determinant one (Hoffmann et al., 2012).

Altogether, these ecosystems are of special interest as they have a great potential in assessing questions on long-term ecology and climate, conservation, forest and fire management, human-environmental interactions, and biotic responses. Here we present a mini-review on the current state of the paleo-research in the Llanos ecoregion and provide directions on future perspectives in the most extensive savanna of northern South America.

A BRIEF HISTORICAL VIEW

In 1799 Alexander von Humboldt and Aimé Bonpland started their expedition along the Orinoco River in Venezuela; they described and collected valuable information about the savannas and the gallery forest, its composition, ecology, and the seasonal contrast in the Venezuelan Llanos (Wulf, 2015). Later on, Humboldt demonstrated and explained how climate strongly influences the spatial distribution pattern of the vegetation. His view of climate as a primary driver paved the way for ecology to center its attention on environmental variations (Pausas and Bond, 2019).

In the nineteenth century began the archeological investigations in the Venezuelan Llanos and just since 1972 in the Colombian Llanos. Since then, several excavation sites in the ecoregion have been studied (Gassón, 2002), providing essential findings, such as population establishments, migrations and land-use interactions. The later is based primarily on pottery, hunting, fishing, maize and manioc cultivation. In the eastern Colombian Llanos, carbonized wood and nuts of palm trees were found, evidencing human settlements since 9,200 cal BP (Barse, 1990). Due to the proximity to Amazonia, the presence of humans is associated with the initial adaptation to the tropical forests between 9,200 and 7,000 cal BP, and later with the adaptation to savannas and forests between 7,000 and 4,000 cal BP that emerged due to a drier climate in the middle and late Holocene (Barse, 1995).

In the western Colombian Llanos and in the piedmont and the high llanos of Venezuela, evidence of occupation/settlements occurred later, around 3,000 BP. Excavations sites in the Upper Ariari river, a tributary of the Guaviare river, suggest that the river was used as a migratory route between Orinoquia and Amazonia. From 950 BP onward, numerous tropical forest groups expanded into the Llanos, reaching their climax in the Middle Orinoco at around 750 BP, displacing other small groups (Zucchi and Denevan, 1980; Zucchi, 1985a,b). Human-environmental practices, mainly agriculture (maize, rice, manioc, palms), have been common since 3,000 BP, in which forest clearance by burning practices probably happened.

To understand the dynamics of past vegetation and climate and land-use interactions, paleoecologists have used pollen as a proxy for more than 100 years, disentangling questions not just in long-term ecology but also in biogeography (Birks, 2019). Several studies aiming to calibrate pollen dispersal and deposition, produce estimates of pollen productivity and/or apply the calibrated models to quantitative reconstruct past land-cover have been carried out mainly in Europe after presenting the LANDCLIM project: LAND cover—CLIMate interactions in NW Europe during the Holocene (Gaillard et al., 2010) and in China (Li et al., 2010, 2020a,b).

In tropical and sub-tropical areas, only a few attempts have been made toward quantitative land-cover reconstructions; South Africa (Duffin and Bunting, 2008), South America (Piraquive-Bermúdez, 2021), Cameroon (Gaillard et al., 2021) and sub-tropical China (Fang et al., 2019; Jiang et al., 2020). However, several paleoecological archives have been collected in Latin America (more than 1,300 fossil and 4,800 modern samples) and Africa (288 fossil sites and 1,985 modern samples), which will be essential for future quantitative studies in those regions of the world. For instance, twelve sedimentary archives of Pleistocene and Holocene ages have been studied in the Llanos ecoregion (**Figure 1** and **Table 1**), from which 11 are restricted to the west and just one to the eastern part of the ecoregion. Hereafter, we synthesize the current state of the paleo-research in Colombia and Venezuela and provide insights into future paleo-research perspectives.

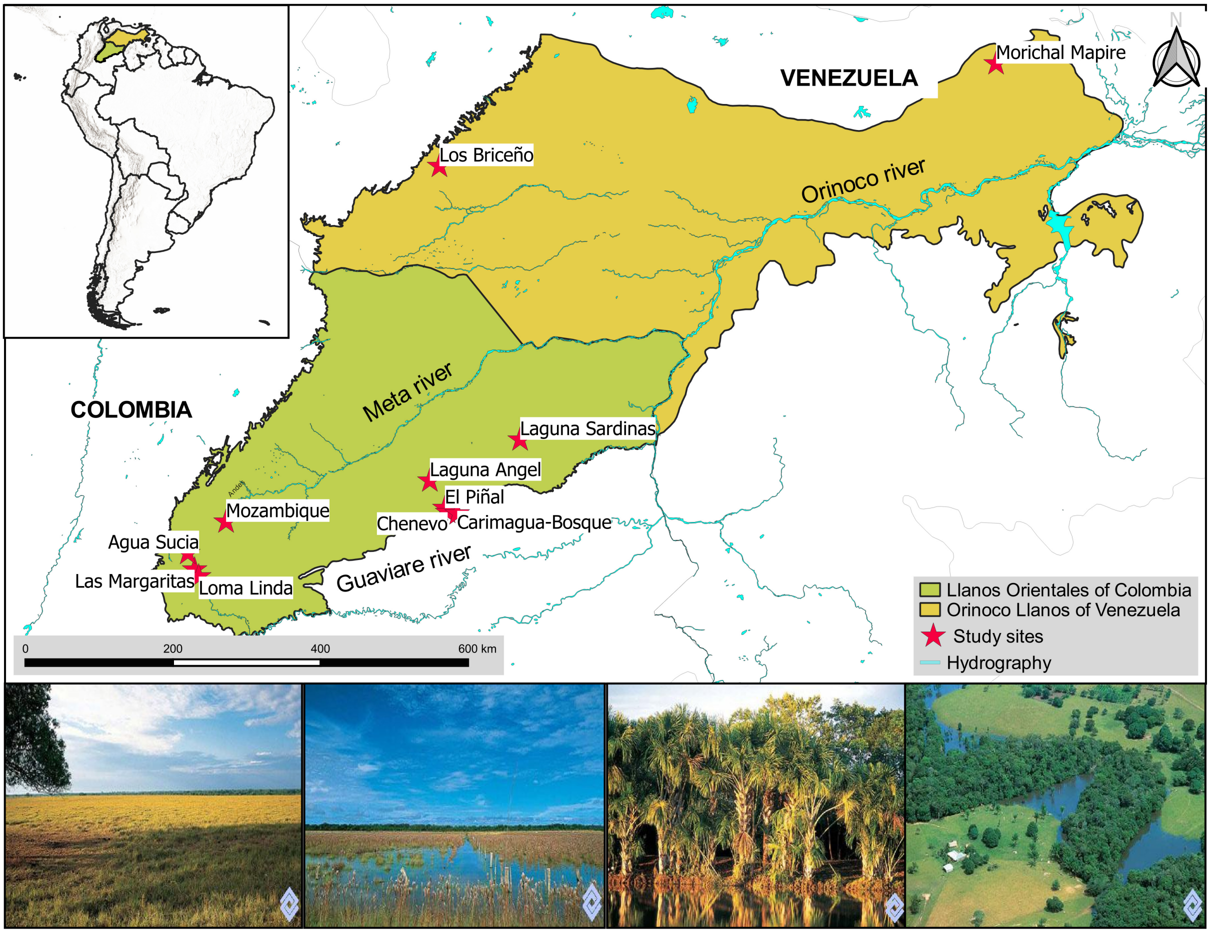

FIGURE 1 | Location of the Llanos of the Orinoco ecoregion in Northern South America together with the study sites reported in Colombia and Venezuela. At the bottom are photographs of the four vegetation types, from left to right: dry savannas, wet savannas, swamps (Morichal) and forests (photograph credits: Santiago Montes Veira and Francisco Forero Bonell).

Current State of the Research in the Llanos Orientales of Colombia

More than 150 years later, after the first Botanical expedition to the Orinoco by Humboldt and Bonpland, van der Hammen visited the Llanos Orientales in 1958, aiming, for the first time, to elucidate part of the history and origin of the tropical savannas by palynological investigations to get an idea on the factors determining the existence of savannas (Wijmstra and van der Hammen, 1966). A sediment core was collected from a lake called Agua Sucia (**Figure 1**), located in a small valley belonging to the incised drainage pattern of the high plain. Agua Sucia sediments date back to around 4,890 cal yr BP, and they might be potentially older, i.e., the base of the core has an extrapolated age of ~6,500 cal yr BP. Their results suggest that the occurrence of open savanna areas in this region happened at around 3,200 cal yr BP, attributed partly to humans, due to felling and burning practices.

In 1996, almost two centuries later, after Humboldt visited the Orinoco Llanos in Venezuela, Behling and Hooghiemstra carried out an expedition in the Llanos Orientales in Colombia, coring several lakes and swamps along a 500 km long transect, starting at the foothills of the Oriental Andes (**Figure 1** and **Table 1**). Laguna Sardinas, the most eastern study site, located at the border of a low-elevated flood plain, shows that between ~13,300 and ~11,700 cal yr BP, savanna vegetation dominated by grassland (Poaceae) and few woody savanna taxa (*Curatella, Byrsonima*) were present, indicating dry climatic conditions with a marked dry season. The increase of *Alchornea* and *Mauritia* palms pointed to a short humid climate from 11,700 to 10,900 cal yr BP. While a marked reduction of forest and gallery forest until 7,340 cal yr BP, together with the substantial increase of savanna herbs, suggests the maximum extension of the grassland and the driest period of the record, probably due to low rainfall rates and/or an extended annual dry season. Between 7,340 and 4,000 cal yr BP the decrease of savanna herbs and the increase of the forest and gallery forest documents a more humid climate than before. The late Holocene (4,000 cal yr BP to the present) vegetation is mainly characterized by the increase of *Mauritia,* an indicator of climatic conditions (high moisture availability) and human impact (agroforestry practices) (Rull and Montoya, 2014;

TABLE 1 | Site details with location, coordinates (lon/lat), core length in cm, estimated calibrate bottom ages in yr BP and site elevation in m above sea level (a.s.l.).

Site	Location	Lon	Lat	Core length cm	Age cal BP	Elevation m a.s.l.
El Piñal	Vichada, COL	70°23′W	4°08′N	72	20,440	180 m
Laguna Sardinas	Vichada, COL	69°28′W	4°58′N	110	13,350	80 m
Laguna Angel	Vichada, COL	70°34′W	4°28′N	193	11,600	200 m
Las Margaritas	Meta, COL	73°26′W	3°23′N	1,000	11,170	290 m
Morichal Mapire	Monagas, VEN	63°40′W	9°33′N	160	10,220	80 m
Loma Linda	Meta, COL	73°23′W	3°18′N	895	9,710	310 m
Carimagua	Vichada, COL	70°14′W	4°04′N	80	9,120	180 m
Chenevo	Vichada, COL	70°21′W	4°05′N	90	8,465	150 m
Agua Sucia	Meta, COL	73°31′W	3°35′N	500	6,560	300 m
Los Briceño	Barinas, VEN	70°27′W	8°18′N	145	4,200	120 m
Mozambique	Meta, COL	73°03′ W	3°58′ N	375	3,833	175 m
Carimagua-Bosque	Vichada, COL	70°13′ W	4°04′ N	65	1,091	180 m

Rangel-Ch, 2019). In Laguna Sardinas, its occurrence is related to the still humid climate and a possible increase in human activities, which is also reflected by an intensified fire regime (Behling and Hooghiemstra, 1998).

About 110 km from Laguna Sardinas is located Laguna Angel. This record shows that savanna grasslands were dominant between 11,590 and 10,400 cal yr BP, accompanied by forest and gallery forest elements (*Alchornea,* Moraceae/Urticaceae, and *Mauritia*), both reflecting a humid period with cooler climatic conditions (Behling and Hooghiemstra, 1998). Until 4,160 cal yr BP, a decline of savanna herbs and an increase of forest and gallery forest suggest an increase in precipitation. The reduction of savanna herbs and the relatively high representation of savanna shrubs and trees until 2,270 cal yr BP have been linked to a wetter climate. In contrast, the increase of *Mauritia* toward the end and the higher fire regime possibly reflect increased human activities.

Two other lakes were cored at about 270 km of the foothills of the Andes and ∼150 km west from Lagunas Sardinas and Angel. Those are Laguna El Piñal and Carimagua, separated 20 km from each other and in a relatively flat area in the central part of the Colombian Llanos. Laguna El Piñal contains the history from the Last Glacial Maximum (LGM). The Late Glacial/Holocene transition is well preserved, while the mid and late Holocene are incomplete. Between ∼20,400 and 11,000 cal yr BP, very little gallery forest and the dominance of savanna taxa reflected a dry period due to low rainfall rates and long dry seasons. At around 11,000 cal yr BP the gallery forest expanded, indicating wetter conditions, where the precipitation was probably higher and the dry season shorter than during the LGM (Behling and Hooghiemstra, 1999). Laguna Carimagua sediments are younger than those from El Piñal, showing that during the early and mid-Holocene, savanna herbs predominated, reaching their maximum extension in which savanna shrubs and trees were uncommon. At the same time, a high fire activity might have occurred, as observed by a high amount of charcoal particles in pollen slides.

The late Holocene history (1,090 cal yr BP to present) and a comparison of the vegetation development have been reconstructed from sediments recovered within the gallery forest near Laguna Carimagua. The results of the short record, known as Laguna Carimagua-Bosque, revealed that the forest was the dominant vegetation during that period until the present, with a changing landscape from *Mauritia* swamps and gallery forest to rich gallery forest with a very low representation of savanna shrubs, trees, and grass savanna. Comparing both records, it is likely that the pollen of savanna vegetation is underrepresented in lake sediments when the lake lies within the gallery forest.

A high-resolution record recovered in the western part of the region, Loma Linda which is 100 km distance from the Andes (**Figure 2**), complements the previous interpretations of the pollen records in the eastern and central part of the Llanos Orientales. Laguna Loma Linda is a lake in the transition zone between the savanna and Amazon rainforest that was part of a former river probably dammed at the beginning of the Holocene (Behling and Hooghiemstra, 2000). During the early Holocene until ∼6,800 cal yr BP, the vegetation was strongly dominated by savanna (Poaceae), suggesting a dry and warm climate. The mid-Holocene was characterized by a marked increase of the gallery forest until ∼3,800 cal yr BP, there savanna trees and shrubs also became more frequent, both indicating a change to a wetter and more stable period. During the late Holocene, the forest started to expand continuously, slowly replacing the savannas. An increasing expansion of the Amazonian rainforest taxa indicates higher precipitation rates. At around 2,500 cal yr BP, grass savanna expanded again, and *Mauritia* palm stands developed. As the palms are used as the main resource to local communities (food and services), their increase indicates an increased human impact due to agroforestry in the savanna region (Rull and Montoya, 2014).

Berrio et al. (2002) added to the research two more lakes, Laguna Chenevo and Laguna Mozambique, at 175 and 80 km from the Eastern Cordillera, respectively. The first lies in an area where patches of savanna, forest, and gallery forest are frequent, while the second is in an area that regularly floods. The early Holocene (8,460–7,000 cal yr BP) at Laguna Chenevo surroundings was characterized by the dominance of savanna herbs. Besides, forest and gallery forest taxa were common (*Alchornea*, *Mauritia*), suggesting a warm and slightly humid climate during that period. Between 7,000 and 2,600 cal yr BP the expansion of the forest and gallery forest occurred,

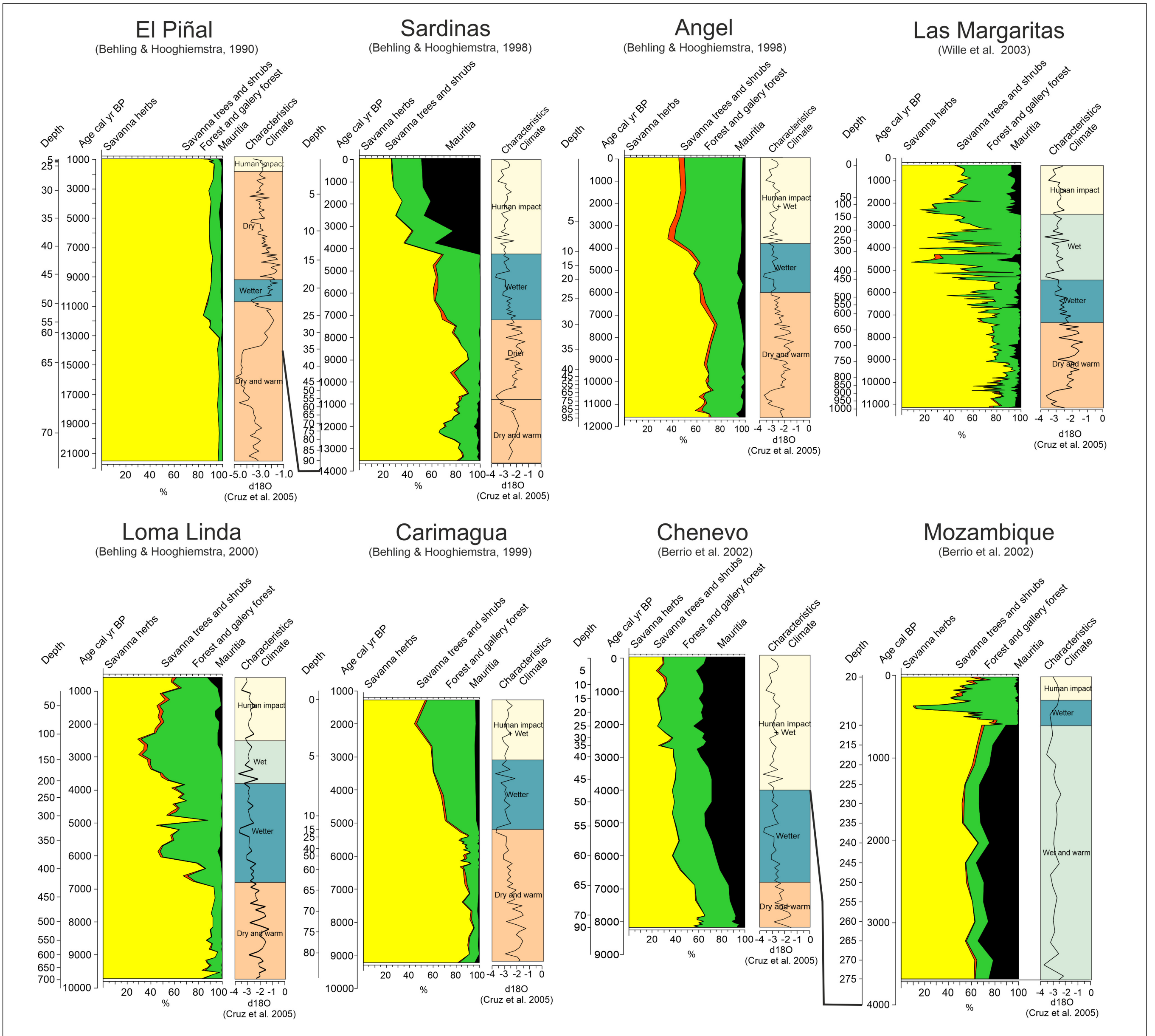

FIGURE 2 | Summary pollen diagrams of the study sites in the Llanos Orientales (available from open source databases); El Piñal (Behling and Hooghiemstra, 1999), Laguna Sardinas and Laguna Angel (Behling and Hooghiemstra, 1998), Las Margaritas (Wille et al., 2003), Loma Linda (Behling and Hooghiemstra, 2000), Carimagua (Behling and Hooghiemstra, 1998), Cheveno and Mozambique (Berrio et al., 2002). Synthetic pollen curves represent different vegetation types: Savanna herbs; main pollen types: Poaceae and Cyperaceae (yellow), savanna trees and shrubs; main pollen types: *Byrsonima*, *Didymopanax* and *Curatella* (orange), Forest and Gallery forest; main pollen types: Arecaceae, *Alchornea,* Moraceae, Melastomataceae (green), *Mauritia* swamps (black) main pollen types: *Mauritia*. Climatic interpretation and characteristics of the identified periods and the climate-based proxy d18O (Cruz et al., 2005) from a stalagmite record in Brazil (Botuverá cave) are plotted; dry and warm (light-orange), wetter (dark blue), wet (light-blue), human impact (pale-orange). Climatic interpretations are based on the original publications. Displayed pollen and d18O data were obtained from Neotoma Paleoecology Database and SISAL, respectively (Atsawawaranunt et al., 2018; Williams et al., 2018).

with a progressive increase of *Mauritia* palms, reflecting wetter conditions. In contrast, the late Holocene documented an increase of charcoal particles, pointing to an intensified fire regime, possibly of anthropogenic origin.

In the western Llanos, Laguna Mozambique revealed that between 3,800 and 650 cal yr BP *Mauritia* swamp forest and gallery forest taxa were abundant around the lake, together with grass savanna, indicating humid climatic conditions. The following period (650–100 cal yr BP) recorded the decline on grass savanna and the expansion of the forest, suggesting a wetter climate than before. While during the last few hundred years, pollen from *Zea mays* and *Mauritia* was recorded, documenting human intervention in the area (Berrio et al., 2002), e.g., increase of cultivated lands.

Almost 20 years ago, the last paleoecological study in the Colombian Llanos was carried out. Wille et al. (2003) analyzed the sediments from Laguna Las Margaritas, located at the south-western part of the Llanos, 75 km from the Eastern Cordillera. With a better age control and a higher resolution, Las Margaritas core (**Figure 2**) shows that between 11,150 and 9,100 cal yr BP, grass savanna dominated the landscape with a poorly developed gallery forest in which fires were common, indicating a warm climate with low precipitation rates and a long dry season. The gallery forest slightly increased between 9,100 and 7,330 cal yr BP. However, from this period until 5,430 cal yr BP, the forest gradually replaced the savanna ecosystem, suggesting a wetter climate. The raiming savanna changed to a wooded one and, together with the forest, dominated the landscape until 2,500 cal yr BP, thus indicating high precipitation rates. The expansion of *Mauritia* at 2,500 cal yr BP and the increase of savanna at 1,000 cal yr BP may indicate both natural (moisture) and human impact (cultivation). Moreover, those general trends of change in the savanna region are well supported by climatic proxies and well documented in stalagmite records in South America, suggesting that during the Late Holocene more precipitation occurred compared to the Mid- and Early Holocene (Cruz et al., 2005; Wang et al., 2007; Bernal et al., 2016).

Current State of the Research in the Orinoco Llanos of Venezuela

The western part of the Llanos ecoregion remains almost unknown regarding its paleoecological history. To date, just two pollen records have been studied, Morichal Mapire and Los Briceño (**Figure 1**). Despite the lack of research, these are the only ones that, besides vegetation, analyzed part of the fire history, providing a better overview of the climate and human impact in the savannas. Nevertheless, the interpretation of the results should be made carefully as, unfortunately, just a few radiocarbon dates were used for the age-depth models.

The first site is called Morichal Mapire, a *Mauritia* swamp community located in the eastern part of the Venezuelan Llanos. During the early Holocene until ∼8,900 cal yr BP, the vegetation mainly represented by savanna (Poaceae, Cyperaceae) and gallery forest taxa (*Cecropia, Phyllanthus, Euterpe/Geonoma*-type) suggests that the climate was warm and humid similar to that of today and was, in consequence, suitable for the growth of *Mauritia* palms. Notwithstanding, its pollen was not detected in the record during this period, allowing the authors to hypothesize that palms populations could have been reduced in the area as a response to the Late Pleistocene arid climates (Leal and Bilbao, 2011). This hypothesis is supported by Rull (1998); however, it might be hampered by diverse ecological traits (pollen dispersion, production, others), making it difficult to draw further conclusions.

During the late Holocene, at the Morical Mapire the presence of *Mauritia* was recorded since ca. 2,200 cal yr BP, a period in which a marsh dominated by Poaceae accompanied by open palm swamps existed, probably also regulated by the high fire frequency until 1,100 cal yr BP, indicating a wetter climate and possible human impact. During the following years, until 320 cal yr BP, a decrease in *Mauritia* palms and an increase of an open savanna dominated by Poaceae and Cyperaceae is related to a reduction of water availability in the swamp, suggesting warmer climatic conditions. From 320 cal yr BP, fires became more frequent, and taxa like *Cecropia* and *Schefflera* increased considerably, reflecting a period of strong human intervention (Leal and Bilbao, 2011).

The second study site is located to the west, in an archeological region about 40 km eastward from the Andes Cordillera in an oxbow lake called Los Briceño (Leal et al., 2019). Between 4,200 and 3,800 cal yr BP, a savanna-forest mosaic was dominant, accompanied by a gallery forest, indicating a humid climate. Fires, possibly of anthropogenic origin, were also common during this period and may have affected the forest in the surroundings of the lake. Later until 2,100 cal yr BP, shifts between forest-dominated and savanna-dominated periods reflected a drier climate or a more seasonal one. During the late Holocene, the increase of aquatics suggests higher lake levels, indicating the onset of a wetter climate, similar to the present. Together, fire frequency/intensity and the occurrence of *Zea mays* in the record reflect a clear sign of human activity in the area of Los Briceño.

Paleoecological Trends in the Llanos Ecoregion

The studies conducted in the last decades in the Llanos ecoregion reveal similar paleoclimatic patterns along the Neotropical savanna, which are at the same time supported by d18O data of South America (**Figure 2**), in which isotope records suggest in general, that for the Late Holocene, the total amount of rainfall was higher when compared to the Mid- and Early Holocene, though its variability was smaller (Cruz et al., 2005; Bernal et al., 2016). Those results evidenced an overall competition between palm forest (*Mauritia*), savanna herbs, and woody vegetation (forest and gallery forest). The pollen diagrams from the Llanos ecoregion suggest that dry herbaceous vegetation prevailed during the LGM, under arid and semi-arid periods (El Piñal), apparently a consequence of the changes in the amplitude of the ITCZ (Behling and Hooghiemstra, 2000; Berrio et al., 2002; Sánchez et al., 2017). During the onset of the Holocene, a slight increase in forest and gallery forest taxa is recorded (Lagunas El Piñal, Sardinas and Angel), suggesting a transition to wet climatic conditions followed by a dry climate.

Several of those records illustrate the overall changes recorded since the early Holocene, indicating that between ∼10,000 and 7,000 cal yr BP, the dominant vegetation type was savannas (Poaceae and Cyperaceae) and forest and gallery forest taxa (*Alchornea*, Moraceae/Urticaceae, and *Mauritia*) were also common but rare, pointing to a warm and slightly humid climate. During the mid-Holocene, after about 7,000 cal yr BP, the gallery forest gradually expanded, suggesting a change to a wetter climate. The proportion of *Mauritia* palms increased markedly after 4,000 or later after 3,000 cal yr BP, possibly driven by higher mean annual precipitation and/or a longer wet season. The start of human occupation remains unclear. However, it has been associated with the expansion of palm swamps (*Mauritia*) varying among locations since around 4,000 or 2,000 cal yr BP, a period in which fires, possibly of anthropogenic origin, were more frequent. Palms provide different services (food, construction material); therefore, it is hypothesized, as is still documented nowadays, that *Mauritia* palms may have been used as a primary resource for humans since the late mid-Holocene (Hooghiemstra and Flantua, 2019).

PERSPECTIVES

Seddon et al. (2014) presented 50 relevant questions divided into six themes to address in paleoecology and Birks (2019) provided an overview of the contributions of Quaternary botany to modern ecology and biography classified into four general components. From both publications, we have taken as a model five topics that we consider most urgent to focus on in the Llanos ecoregion future paleo-research: (1) Long term ecology and climate, (2) Quantitative paleoecology, (3) Conservation, forest and fire management, (4) Human-environmental interactions and (5) Biotic responses. We provide a number of research questions to be answered and the possible directions and challenges that can be encountered while carrying out paleoecological studies in the Llanos.

Long Term Ecology and Climate

1. How climate change influenced the dynamics of vegetation and fire?
2. Are the changes in the vegetation influenced by factors such as organic and inorganic components in the soils?

To address those questions, we suggest that future investigations should prioritize high-resolution multi-proxy studies, including but not limited to pollen, charcoal, geochemistry, sedimentary ancient DNA (sedaDNA), and diatoms, in which detailed chronological analyses is conducted. The latter is of special importance, as good chronological control is essential for further applications such as quantitative paleoecology.

Moreover, interdisciplinary research should be pursued, especially between archeology, paleoecology, fire-ecology, botany and climatology, as they constitute a valuable tool for understanding the natural variability of the Orinoquia.

Quantitative Paleoecology

3. How is the representation of plant diversity in the pollen assemblages captured by modern surface and moss samples among savannas and forest ecosystems?
4. Can we apply pollen productivity estimate values (PPE) to quantitative interpret fossil pollen records from the neotropical savannas of northern South America?
5. How will these ecosystems change under future climatic scenarios?

Reliable paleoecological data is necessary to produce and validate climatic models (paleo-simulations), which will at the same time help improve their capacity in predicting past and future climate change scenarios (Gaillard et al., 2008; Harrison et al., 2020). However, in a relatively little-studied region, there is a lack of knowledge about ecological traits (for example, pollen productivity, dispersal and pollination mode), which are important for testing ecological hypotheses, and a forehand step for elaborating climatic models. Therefore, increasing the coverage and spatiotemporal resolution will improve our understanding of the causes and dynamics of past changes across a broader timescale. Hence, we encourage new research toward land-cover reconstructions by calibrating pollen dispersal and depositional models (ERV-models), estimating pollen productivity (PPE) of the major savanna-forest taxa, testing their reliability and applying the calibrated models to new/old pollen records through the Landscape Reconstruction Algorithm (LRA). However, applying these methods and models is still a challenge for the southern hemisphere and, in general, for the tropics, where the major challenge corresponds to the estimation of reliable PPEs, due to factors such as landscape heterogeneity, the effect of non-stationary vegetation and pollen transport being mainly entomophilous (Gaillard et al., 2021).

Conservation, Forest, and Fire Management

6. What is the role of disturbances, particularly fire, in the savanna-forest ecosystems of northern South America?

According to Birks (2019) they are different applications and contributions of paleoecological studies to the conservation of ecosystems, among them are (1) the assessment of naturalness and fragility of a given ecosystem, (2) evaluation of the conservation status of endangered species through the contribution of information about the causes that lead to the decline of certain taxa, (3) the creation of data as a baseline on the composition and function of ecosystems in the past.

Therefore, by studying Holocene dynamics of fires in the Llanos, their periodicity, magnitude and intensity on a decadal or sub-decadal scale will enable paleo-researchers to communicate the ecological importance of fires to conservation/land-management practitioners and help them to understand past, present and future scenarios under a changing climate, providing guidelines toward conservation directions.

Human-Environmental Interaction

7. How has the vegetation reacted to anthropogenic disturbances during the Holocene in this region?

Understanding and quantifying land-use interactions based on the fossil record should be addressed with the already available archeological information, which is extensive across the region compared to paleoecological studies (Gassón, 2002). We recommend archeological data to be used in conjunction with paleo-vegetation and paleo-fire data to reconstruct past land cover qualitative and quantitative, particularly in an ecosystem in which the absence of the last ∼3,000 cal yr BP in the sedimentary record is common, a period in which agricultural practices rapidly expanded across the region (Berrio et al., 2000, 2002; Hooghiemstra and Flantua, 2019).

Biotic Responses

8. Was the expansion/contraction of *Mauritia* swamps and in general forest ecosystems synchronous across the region and influenced by the changes in the amplitude and magnitude of the ITCZ?

Among the major types of biotic responses to environmental changes are the distributional range shifts (dispersal and range expansion or contraction). A better overview of these responses in a mosaic of savanna-forest dominated ecosystems will be possible through the study of combined sciences. For instance, independent climatological data is needed, as the already available speleothem data of South America (Deininger et al., 2019), well-dated high-resolution (decadal or sub-decadal) pollen records from different locations, covering, if possible, the Holocene period or part of it and as well detailed fire records.

CHALLENGES OF PALEO-RESEARCH IN THE LLANOS AND FINAL RECOMMENDATIONS

While attempting to carry out paleo-research in the Llanos ecoregion, scientists will encounter different challenges, and this can be (i) difficult or limited access to natural areas due to intern conflicts, both in Venezuela and Colombia (particularly the northern area) and (ii) permit request-bureaucracy, that can take up to some months. Therefore, contacting the national authorities to get information on accessibility and prepare documents with sufficient time prior to starting a research project is highly recommended. Ideally, research projects should be focused on the less explored areas of the Llanos, such as in the Venezuelan side and the Central and Eastern Llanos of Colombia. Finally, we advise on best practices with local authorities and involving local scientists if foreign teams lead the research projects. This will benefit the research development by speeding up times in fieldwork and permit requests, reducing cost, and building up a local team that will be encouraged to continue with similar projects in the southern hemisphere.

AUTHOR CONTRIBUTIONS

DP-B: conceptualization, literature reviews and writing, and original draft review and editing. HB: review and editing. Both authors contributed to the article and approved the submitted version.

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REFERENCES

Atsawawaranunt, K., Comas-Bru, L., Amirnezhad Mozhdehi, S., Deininger, M., Harrison, S. P., Baker, A., et al. (2018). The SISAL database: a global resource to document oxygen and carbon isotope records from speleothems. *Earth System Sci. Data* 10, 1687–1713. doi: 10.5194/essd-10-1687-2018

Barse, W. P. (1990). Preceramic occupations in the Orinoco river valley. *Science* 250, 1388–1390. doi: 10.1126/science.250.4986.1388

Barse, W. P. (1995). "El período arcaico en el Orinoco y su contexto en el norte de *Sudamerica*," in *Ambito y Ocupaciones Tempranas de la América Tropical*, eds I. Cavelier and S. Mora Camargo (Bogotá: Fundación Erigaie, Instituto Colombiano de Antropología), 154.

Behling, H., and Hooghiemstra, H. (1998). Late quaternary palaeoecology and palaeoclimatology from pollen records of the savannas of the llanos orientales in Colombia. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 139, 251–267. doi: 10.1016/S0031-0182(97)00139-9

Behling, H., and Hooghiemstra, H. (1999). Environmental history of the Colombian savannas of the llanos orientales since the last glacial maximum from lake records el pinal and carimagua. *J. Paleolimnol.* 21, 461–476. doi: 10.1023/A:1008051720473

Behling, H., and Hooghiemstra, H. (2000). Holocene Amazon rainforest–savanna dynamics and climatic implications: high-resolution pollen record from Laguna Loma Linda in eastern Colombia. *J. Quat. Sci.* 15, 687–695. doi: 10.1002/1099-1417(200010)15:7<687::aid-jqs551>3.0.co;2-6

Bernal, J. P., Cruz, F. W., Stríkis, N. M., Wang, X., Deininger, M., Catunda, M. C. A., et al. (2016). High-resolution Holocene South American monsoon history recorded by a speleothem from Botuverá Cave. Brazil *Earth Planet Sci. Lett.* 450, 186–196. doi: 10.1016/j.epsl.2016.06.008

Berrio, J. C., Hooghiemstra, H., Behling, H., Botero, P., and Van der Borg, K. (2002). Late-quaternary savanna history of the Colombian llanos orientales from lagunas chenevo and mozambique: a transect synthesis. *Holocene* 12, 35–48. doi: 10.1191/0959683602h1518rp

Berrio, J. C., Hooghiemstra, H., Behling, H., and van der Borg, K. (2000). Late holocene history of savanna gallery forest from carimagua area, Colombia *Rev. Palaeobot. Palynol.* 111, 295–308. doi: 10.1016/S0034-6667(00)00030-0

Birks, H. J. B. (2019). Contributions of quaternary botany to modern ecology and biogeography. *Plant Ecol. Divers.* 12, 189–385. doi: 10.1080/17550874.2019.1646831

Convention on Wetlands, Couroble, M., Davidson, N., Dinesen, L., Fennessy, S., Galewski, T., et al. (2021). *Global Wetland Outlook: Special Edition 2021*. Gland: Secretariat of the Convention of Wetlands.

Cruz, F. W., Burns, S. J., Karmann, I., Sharp, W. D., Vuille, M., Cardoso, A. O., et al. (2005). Insolation-driven changes in atmospheric circulation over the past 116,000 years in subtropical Brazil. *Nature* 434, 63–66. doi: 10.1038/nature03365

Deininger, M., Ward, B. M., Novello, V. F., and Cruz, F. W. (2019). Late quaternary variations in the south american monsoon system as inferred by speleothems—new perspectives using the SISAL database. *Quaternary* 2:6. doi: 10.3390/quat2010006

Duffin, K. I., and Bunting, M. J. (2008). Relative pollen productivity and fall speed estimates for southern African savanna taxa. *Veg. Hist. Archaeobot.* 17, 507–525. doi: 10.1007/s00334-007-0101-2

Etter, A. (1998). "Mapa general de ecosistemas de Colombia," in *Informe Nacional Sobre el Estado de la Biodiversidad en Colombia 1997: Causas de Pérdida de Biodiversidad*, eds M. E. Chaves and N. Arango (Bogotá:

Instituto de Investigación de Recursos Biológicos Alexander von Humboldt), 223.

Fang, Y., Ma, C., and Bunting, M. J. (2019). Novel methods of estimating relative pollen productivity: A key parameter for reconstruction of past land cover from pollen records. *Progress in Physical Geography* 43, 731–753. doi: 10.1177/0309133319861808

Gaillard, M.-J., Githumbi, E., Achoundong, G., Lézine, A.-M., Hély, C., Lebamba, J., et al. (2021). "The challenge of pollen-based quantitative reconstruction of Holocene plant cover in tropical regions: a pilot study in Cameroon," in *Quaternary Vegetation Dynamics The African Pollen Database*, eds J. Runge, W. D. Gosling, A.-M. Lézine, and L. Scott (Boca Raton, FL: CRC Press).

Gaillard, M.-J., Sugita, S., Bunting, M. J., Middleton, R., Broström, A., Caseldine, C., et al. (2008). The use of modelling and simulation approach in reconstructing past landscapes from fossil pollen data: a review and results from the POLLANDCAL network. *Veg. Hist. Archaeobot.* 17, 419–443. doi: 10.1007/s00334-008-0169-3

Gaillard, M.-J., Sugita, S., Mazier, F., Trondman, A.-K., Broström, A., Hickler, T., et al. (2010). Holocene land-cover reconstructions for studies on land cover-climate feedbacks. *Clim. Past* 6, 483–499. doi: 10.5194/cp-6-483-2010

Gassón, R. (2002). Orinoquia: the archaeology of the orinoco river basin. *J. World Prehist.* 16, 237–311. doi: 10.1023/A:1020978518142

Harrison, S. P., Gaillard, M.-J., Stocker, B. D., Vander Linden, M., Klein Goldewijk, K., Boles, O., et al. (2020). Development and testing scenarios for implementing land use and land cover changes during the holocene in earth system model experiments. *Geosci. Model Dev.* 13, 805–824.

Hoffmann, W. A., Geiger, E. L., Gotsch, S. G., Rossatto, D. R., Silva, L. C. R., Lau, O. L., et al. (2012). Ecological thresholds at the savanna-forest boundary: how plant traits, resources and fire govern the distribution of tropical biomes. *Ecol. Lett.* 15, 759–768. doi: 10.1111/j.1461-0248.2012.01789.x

Hooghiemstra, H., and Flantua, S. G. A. (2019). "Colombia in the Quaternary: an overview of environmental and climatic change," in *The Geology of Colombia.* Publicaciones Geológicas Especiales, eds J. Gómez and A. O. Pinilla-Pachon (Bogotá: Servicio Geológico Colombiano), 43–95. doi: 10.32685/pub.esp.38.2019.02

Jaramillo-J, A., Villamizar, V. A., and Vélez, A. (2019). "Geología del noreste del Río Cravo Norte (Margen Izquierda), Colombia," in *Colombia Diversidad Biótica XX: Territorio Sabanas y Humedales de Arauca (Colombia)*, eds J. O. Rangel-Ch, M. G. Andrade, C. Jarro, and G. Santos (Bogotá: Universidad Nacional de Colombia), 852.

Jaramillo-J, A., Villamizar-M, V. A., and Vélez, A. (2019b). "geología y geomorfología en el territorio de las selvas transicionales de cumaribo, vichada (Colombia)," in *Colombia Diversidad Biótica XIV: Selvas transicionales de Cumaribo (Vichada - Colombia)*, eds J. O. Rangel-Ch, M. G. Andrade, C. Jarro, and G. Santos (Colombia: Universidad Nacional de Colombia), 702.

Jiang, F., Xu, Q., Zhang, S., Li, F., Zhang, K., Wang, M., et al. (2020). Relative pollen productivities of the major plant taxa of subtropical evergreen–deciduous mixed woodland in China. *J. Quat. Sci.* 35, 526–538. doi: 10.1002/jqs.3197

Lasso, C. A., Rial, A., Colonnello, G., Machado-Alisson, A., and Trujillo, F. (eds) (2014). "XI. humedales de la orinoquia (Colombia-Venezuela)," in *a. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt (IAvH). Serie Editorial Recursos Hidrobiológicos y Pesqueros Continentales de Colombia*, ed. Carlos A. Lasso (Bogotá: Colombia Instituto de Investigación de Recursos Biológicos Alexander von Humboldt), 303.

Leal, A., and Bilbao, B. (2011). Cambios de vegetación durante el holoceno tardío en un morichal de los Llanos del Orinoco Venezuela. *Acta. Bot. Venez.* 34, 237–256.

Leal, A., Gassón, R., Behling, H., and Sánchez, F. (2019). Human-made fires and forest clearance as evidence for late holocene landscape domestication in the Orinoco Llanos (Venezuela). *Veget. Hist. Archaeobot.* 28, 545–557. doi: 10.1007/s00334-019-00713-w

Li, B., Nychka, D. W., and Ammann, C. M. (2010). The value of multiproxy reconstruction of past climate. *J. Am. Stat. Assoc.* 105, 883–895.

Li, F., Gaillard, M.-J., Cao, X., Herzschuh, U., Sugita, S., Tarasov, P. E., et al. (2020a). Towards quantification of Holocene anthropogenic land-cover change in temperate China: a review in the light of pollen-based REVEALS reconstructions of regional plant cover. *Earth Sci. Rev.* 203:103119. doi: 10.1016/j.earscirev.2020.103119

Li, F., Gaillard, M.-J., Sugita, S., Cao, X., Herzschuh, U., Zhao, Y., et al. (2020b). "REVEALS-based reconstruction of Holocene vegetation abundance in temperate China: new insights on past human-induced land-cover change for climate modelling," in *Proceedings of the EGU General Assembly 2020, Online, 4–8 May 2020, EGU2020-9417*. doi: 10.5194/egusphere-egu2020-9417

Minorta-Cely, V., Rangel-Ch, J. O., Castro-L, F., and Aymard, G. (2019). "La vegetación de la serranía de Manacacías (Meta) Orinoquía Colombiana," in *Colombia Diversidad Biótica XVII: La Región de la Serranía de Manacacías (Meta) Orinoquía Colombiana*, eds J. O. Rangel-Ch, M. G. Andrade, C. Jarro, and G. Santos (Bogotá: Universidad Nacional de Colombia), 660.

Pausas, J. G., and Bond, W. J. (2019). Humboldt and the reinvention of nature. *J. Ecol.* 107, 1031–1037. doi: 10.1111/1365-2745.13109

Piraquive-Bermúdez, D. (2021). *Vegetation and Fire History in Araucaria Forest and Grasslands, Southern Brazil*. Gottingen: Georg-August-Universität Göttingen.

Rangel-Ch, J. O. (2019). "Ecosistemas de la Orinoquía Colombiana," in *Colombia Diversidad Biótica XIV: Selvas Transicionales de Cumaribo (Vichada – Colombia)*, eds J. O. Rangel-Ch, M. G. Andrade, C. Jarro, and G. Santos (Bogotá: Universidad Nacional de Colombia-Instituto de Ciencias Naturales), 702.

Romero-Ruiz, M. H. (2011). *Influence of Land Use, Climate And Topography On The Fire Regime in the Eastern Savannas of Colombia*. Available online at: https://leicester.figshare.com/articles/thesis/Influence_of_land_use_climate_and_topography_on_the_fire_regime_in_the_Eastern_Savannas_of_Colombia/10102670/1 (accessed January 31, 2022).

Romero-Ruiz, M. H., Flantua, S. G. A., Tansey, K., and Berrio, J. C. (2012). Landscape transformations in savannas of northern South America: land use/cover changes since 1987 in the llanos orientales of Colombia. *Appl. Geogr.* 32, 766–776. doi: 10.1016/j.apgeog.2011.08.010

Rull, V. (1998). Biogeographical and evolutionary considerations of Mauritia (Arecaceae), based on palynological evidence. *Rev. Palaeobot. Palynol.* 100, 109–122. doi: 10.1016/S0034-6667(97)00060-2

Rull, V., and Montoya, E. (2014). Mauritia flexuosa palm swamp communities: natural or human-made? A palynological study of the Gran Sabana region (northern South America) within a neotropical context. *Q. Sci. Rev.* 99, 17–33. doi: 10.1016/j.quascirev.2014.06.007

Sánchez, F., Fernández, J., Gassón, R., Bezada, M., and Leal, A. (2017). "Paleoecología y ocupación humana durante el Holoceno en los Llanos del Orinoco: una revisión y nuevos datos," in *BioLlania, Ezequiel Zamora*, ed. G. Aymard (Barinas: Universidad Nacional Experimental de los Llanos Occidentales), 297–333.

Seddon, A. W. R., Mackay, A. W., Baker, A. G., Birks, H. J. B., Breman, E., Buck, C. E., et al. (2014). Looking forward through the past: identification of 50 priority research questions in palaeoecology. *J. Ecol.* 102, 256–267. doi: 10.1111/1365-2745.12195

Wang, X., Auler, A. S., Edwards, R. L., Cheng, H., Ito, E., Wang, Y., et al. (2007). Millennial-scale precipitation changes in southern Brazil over the past 90,000 years: PAST PRECIPITATION CHANGE IN BRAZIL. *Geophys. Res. Lett.* 34:L23701. doi: 10.1029/2007GL031149

Wijmstra, T. A., and van der Hammen, T. (1966). Palynological data on the history of tropical savannas in northern South America. *Leidse Geologische Meded.* 38:23.

Wille, M., Hooghiemstra, H., van Geel, B., Behling, H., de Jong, A., and van der Borg, K. (2003). Submillennium-scale migrations of the rainforest–savanna boundary in Colombia: 14C wiggle-matching and pollen analysis of core las margaritas. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 193, 201–223. doi: 10.1016/S0031-0182(03)00226-8

Williams, J. W., Grimm, E. C., Blois, J. L., Charles, D. F., Davis, E. B., Goring, S. J., et al. (2018). The Neotoma Paleoecology Database, a multiproxy, international, community-curated data resource. *Quaternary Research* 89, 156–177. doi: 10.1017/qua.2017.105

Wulf, A. (2015). *The Invention of Nature?: Alexander Von Humboldt's New World*. New York, NY: Knopf (US).

Xi, Y., Peng, S., Ciais, P., and Chen, Y. (2021). Future impacts of climate change on inland Ramsar wetlands. *Nat. Clim. Chang.* 11, 45–51. doi: 10.1038/s41558-020-00942-2

Zucchi, A. (1985a). Evidencias arqueológicas sobre grupos de posible lengua caribe. *Antropológica* 63–64, 23–44.

Zucchi, A. (1985b). "Recent evidence for pre-Columbian water management systems in the western Llanos of Venezuela," in *Prehistoric Intensive Agriculture in the Tropics*, ed. I. S. Farrington (Oxford: BAR International), 167–180.

Zucchi, A., and Denevan, W. M. (1980). *Campos Elevados e Historia Cultural Prehispánica en los Llanos Occidentales de Venezuela*. Caracas: Universidad Católica Andrés Bello, Instituto de Investigaciones Históricas.

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