Rethinking glacial retreat and postglacial expansion of the Netropical palm *Mauritia*

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Abstract

This paper presents an unconventional perspective on the glacial retraction and postglacial expansion of the lowland Neotropical palm *Mauritia flexuosa* during the last glacial cycle. The classical view holds that this palm was confined to multiple wet refugia during the Last Glacial Maximum (LGM), owing to purported Neotropical-wide arid climates. From these refugia, *M. flexuosa* is thought to have expanded across much of tropical South America in postglacial times in response to a hypothetical increase in moisture. Here, we reconsider the available paleoecological, phylogeographic, paleoclimatic and eustatic evidence to propose an alternative scenario. Paleoecological and phylogeographic data are consistent with widespread glacial refugia; however, paleoclimatic reconstructions indicate that general cooling, rather than the assumption of broad Neotropical aridity, played a greater role in driving *M. flexuosa* retraction to warm refugia up to ~200 m elevation. Within this framework, the continental shelf—exposed during the LGM—would have represented an unexpected landmass for sustaining glacial *Mauritia* refugia. Postglacial expansion would have been driven mainly by Holocene warming. This new perspective integrates elements of both the refugial and the divergence–vicariance hypotheses, two classical competing explanations for Neotropical biogeography. The evidence suggests that these hypotheses are best viewed as complementary rather than mutually exclusive.

Keywords

Last Glacial Maximum, *Mauritia*, Neotropics, Palynology, Paleoclimatology, Postglacial, Refugia

Introduction

Mauritia flexuosa L.f. is among the most common and widespread palm species in the Neotropics, with an estimated population of around 1.5 billion individuals (ter Steege et al., 2013). It thrives across diverse ecosystems—including rainforests, gallery forests, savannas, forest-savanna ecotones/mosaics and coastal forests—either as part of mixed vegetation or in dense, monospecific stands. This palm prefers warm, humid lowland environments and typically grows from near sea level up to about 1000 meters in elevation. It is commonly found in freshwater-flooded soils, such as along riverbanks, lake edges, valley floors and coastal marshes behind mangroves, as they cannot tolerate saline conditions (Vegas-Vilarrúbia et al., 2007). *M. flexuosa* holds significant cultural and practical value for human populations, particularly indigenous groups who often refer to it as the "tree of life." While its fruit is especially prized, nearly every part of the palm is used—for food, shelter, decoration, fiber, medicine, rituals, and more. For further information on its uses and cultural importance, see Rull & Montoya (2014) and Virapongse et al. (2017).

Bogotá-Ángel et al. (2021) suggest that the ancestral forms of *Mauritia* originated in Africa during the Cretaceous period and later spread to South America and India in the Paleocene. However, the global cooling event during the Eocene-Oligocene transition (EOT) caused the extinction of *Mauritia* in India and a sharp decline in its diversity in Africa, where it ultimately disappeared in the Oligocene. As a result, *Mauritia* has been confined to the Neotropics since the Miocene. Today, *M. flexuosa* is found in the lowland regions of northern South America, particularly within the Orinoco, Amazon, and neighboring basins, ranging roughly from 12°N to 24°S (Fig. 1).

From a paleoecological standpoint, *Mauritia* pollen is frequently found in Neotropical sediment records from both the last glacial and postglacial periods and is widely used as an indicator of lowland wetlands (Rull, 1998). It has also been used to support the refugial hypothesis (RH) of Neotropical diversification and biogeography (Rull & Montoya, 2014; de Lima et al., 2014). The RH proposes that widespread Neotropical aridity during the last glacial period led to the fragmentation of Neotropical lowland forests into isolated patches, or refugia, surrounded by a sea of savannas—thereby promoting vicariance. During the subsequent wetter postglacial period, these forests likely expanded and reconnected, encouraging gene flow (Haffer, 1969; Prance, 1982; Whitmore & Prance, 1987; Haffer & Prance, 2001).

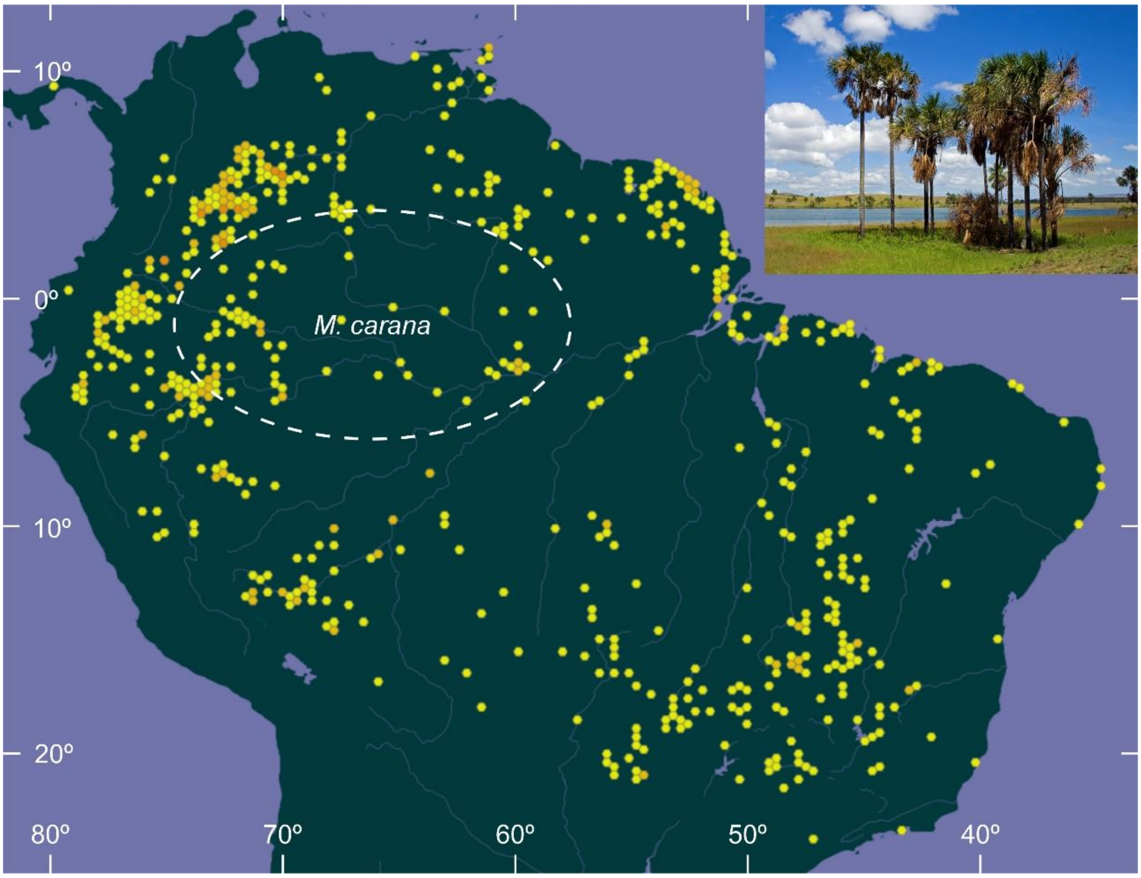

Figure 1. Map of northern South America showing the current distribution of *Mauritia flexuosa* (orange/yellow dots). The distribution area of *M. carana* is indicated by a dotted line. Downloaded from the Global Biodiversity Information Facility (GBIF) (https://www.gbif.org/; last accessed Jan 28, 2025).

The RH has been questioned due to the lack of strong evidence supporting the presumed widespread aridity during the last glacial period (Colinvaux et al., 1996, 2000). As an alternative, the disturbance–vicariance hypothesis (DVH) suggests that lowland forests remained continuous during the last glaciation but underwent changes in taxonomic composition, driven by the downslope migration of sensitive montane species in response to cooling, moderate reductions in precipitation, and lower atmospheric CO_2 levels (Bush, 1994). Building on Gentry's (1982) ideas, supporters of the DVH highlighted the role of the Andean uplift and the long-term stability of Amazonian forests throughout the Neogene as key drivers of present-day Neotropical diversity and biogeography (Colinvaux & De Oliveira, 2001).

This commentary reexamines the glacial and postglacial dynamics of *Mauritia* within the context of the RH-DVH debate. As noted above, spatiotemporal patterns of this palm during the last glacial cycle have been considered mainly within the RH framework, while their relevance to the DVH has received limited attention. The discussion is based on several independent evidence-based available reconstructions: (i) biogeographical shifts over time are based on the available pollen records, (ii) genetic differentiation of current populations is derived from phylogeographical studies, (iii) paleoclimates are addressed using isotopic analyses and (iv) potential unanticipated glacial refugia are derived from eustatic patterns.

Pollen records

A previous paleoecological synthesis identified nearly 60 Neotropical records of *Mauritia* pollen across the range of *M. flexuosa*, spanning elevations from near sea level to 1040 m elevation and covering the period from the Late Pleistocene to the present (Rull & Montoya, 2014). In this commentary, the dataset has been revised and updated by incorporating a dozen additional sequences published over the last decade (Table 1). Temporal trends of *Mauritia* pollen across all sites are illustrated in a composite figure, organized by time intervals and percentage classes to facilitate visualization (Fig. 2). The updated dataset confirms the overall picture presented in the previous compilation, which is outlined below.

The earliest pollen evidence, dating to just before the Last Glacial Maximum (LGM), revealed the presence of *Mauritia* at several locations, with some meaningful percentages to the south. During the LGM, *Mauritia* pollen persisted in a few lowland sites but declined to less than 1% at all of them. It should be noted that LGM sediments are lacking or are difficult to date in a number of sites, which limits the ability to develop a more detailed picture. In the Lateglacial, the distribution broadened east to west, and some sites showed modest increases in pollen percentages. This trend intensified during the Early Holocene, coinciding with a rapid global warming and increased regional rainfall (Haug et al., 2001). The widest distribution occurred in the Middle Holocene during the Holocene Thermal Maximum (HTM), aligned with peak precipitation levels. In the Late Holocene, *Mauritia* became more abundant in the western region despite ongoing general aridification and stable temperatures (Haug et al., 2001). The Late Holocene eastern-western contrast is significantly emphasized in the updated data set with respect to the former compilation by Rull & Montoya (2014).

Rivers and humans have been proposed as the main dispersal agents of *Mauritia* during its postglacial expansion (Sander et al., 2017). Human activity has been especially influential over the past 2000 years, particularly in marginal forest–savanna mosaics and ecotones, where agroforestry practices including, selective burning, created favorable conditions for *Mauritia* development (Rull & Montoya, 2014; Maezumi et al., 2022).

Overall, the data suggest a postglacial expansion from scattered lowland refugia (or microrefugia; Rull, 2009) where *Mauritia* may have survived the glacial period. While the biogeographic pattern aligns with the RH, the specific environmental factors driving glacial retreat and postglacial expansion remain uncertain using only pollen data. Despite this, most individual *Mauritia* records compiled here are interpreted primarily in terms of moisture availability.

Table 1. Localities with glacial/postglacial records of *Mauritia* pollen published after the compilation by Rull & Montoya (2014).

Code	Locality	Country	Latitude	Longitude	Elevation (m)	References
En	Encantada	Venezuela	04°42’38”N	61°05’03”W	857	Ballesteros et al. (2014)
Tp	Tepequém	Brazil	03°47’31”N	61°42’16”E	635	Rodríguez-Zorro et al. (2017)
SJ	São José	Brazil	17°04’47”S	45°06’40”W	680	Cassino et al. (2018)
Tg	Tigre	Venezuela	09°30’08”N	62°40’55”W	13	Montoya et al. (2019)
Vs	Versalles	Bolivia	12.66’S	63.38°W	146	Maezumi et al. (2022)
LA	Los Amigos	Peru	12.56°S	70.12°W	ND	Wang et al. (2022)
Os	Oasis	Brazil	07°13’53”S	39°28’31”W	737	Freire et al. (2024)

Ch	Chamu	Brazil	07°24’28”S	39°12’11”W	763	Freire et al. (2024)
Ps	Pescador	Venezuela	ND	ND	ND	Pocknall & Jarzen (2024)
SR	San Roque	Peru	04°26’40”S	74°34’07”W	ND	Sassoon et al. (2024)
Ys	Yasuní	Ecuador	00°40’59”S	76°23’52”W	288	Spater et al. (2024)

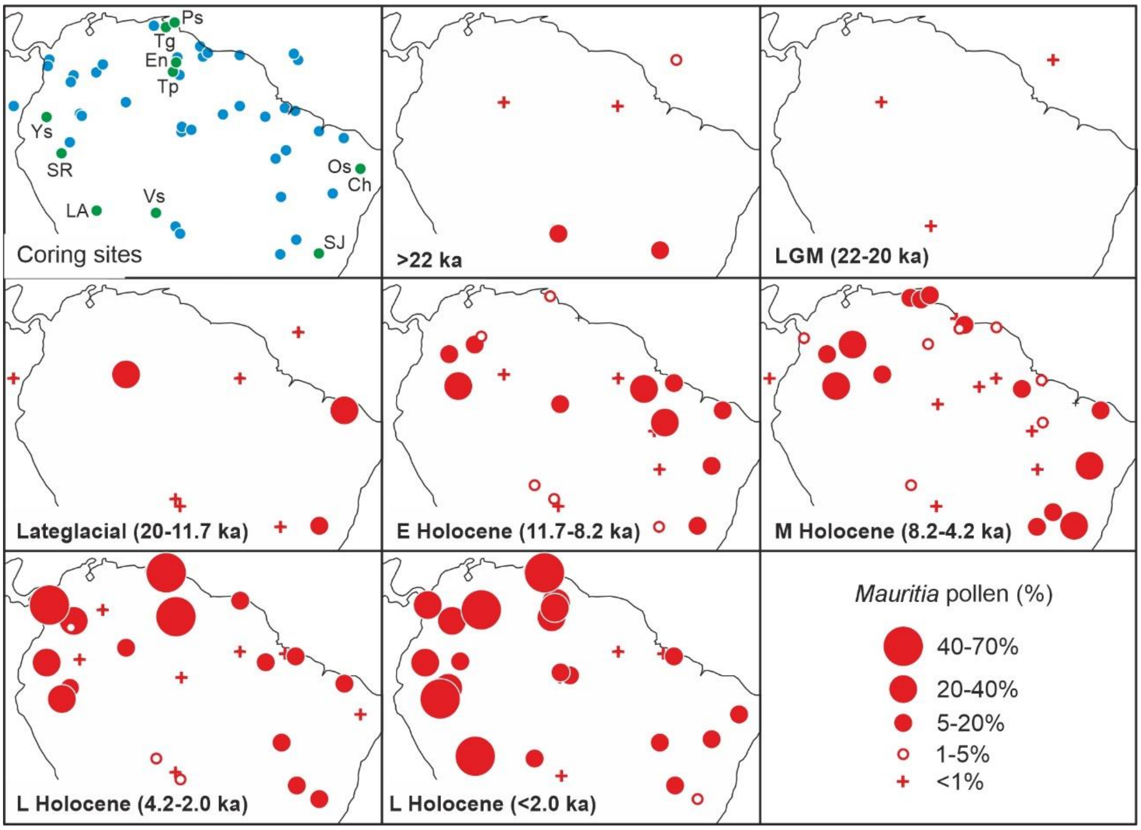

Figure 2. Map of northern South America showing the localities where *Mauritia* pollen has been identified in Late Pleistocene and Holocene sedimentary records. Blue coring sites (upper left) correspond to the initial compilation by Rull & Montoya (2014); see that publication for further details. Green coring sites represent new additions included in the update presented in this paper (refer to Table 1 for abbreviations and further information). Red circles indicate pollen percentage classes, as shown in the scale at the lower right.

Phylogeography

Only two species of *Mauritia*—*M. flexuosa* L.f. and *M. carana* Wallace—are currently recognized (Smith, 2015). The former is by far the more dominant, while the latter has a more restricted distribution and is confined to sandy soils along some northern Amazon tributaries, especially within the Rio Negro basin (Fig. 1). This distribution pattern shows little differentiation across the vast continental expanse of tropical South America. However, intraspecific genetic diversity within *M. flexuosa* is biogeographically significant. For example, de Lima et al. (2014) found substantial genetic differentiation among populations from different river basins in the eastern Amazon, attributing this to the classical aridity-driven RH. Similar patterns of genetic diversity have been observed in parts of the western basin and were explained by low genetic connectivity among populations, though without specific reference to the RH (Montúfar et al., 2019). In the central Amazon Basin, genetic diversity in *M. flexuosa* also aligns with river basin boundaries and water flow direction, both of which influence gene flow among populations, consistent with the classical RH (Sander et al., 2017).

Phylogeographical studies conducted across the entire distribution range of *M. flexuosa* have confirmed high intraspecific genetic differentiation, not only among river basins but also among biomes (rainforest, savanna), and linked this pattern to the RH (Melo et al., 2018). Despite this genetic diversity, low differentiation was found in loci under selection by environmental drivers, especially hydroclimate, and most populations from different ecosystems shared similar allele frequency distributions (Melo et al., 2020). The authors suggested that this genetic homogeneity results from the local adaptation of *M. flexuosa* to swampy microhabitats, regardless of broader bioclimatic differences.

It could be asked whether intraspecific differentiation within *M. flexuosa* reflects postglacial expansion after the LGM or repeated contraction–expansion events during the glacial–interglacial cycles of the Pleistocene. It would be particularly interesting to determine the chronology of the differentiation between *M. flexuosa* and *M. carana*, but no studies have addressed this divergence. Recent simulations by Melo et al. (2018), using microsatellite markers, suggest that the current demographic structure across the Amazon Basin is consistent with expansion of *M. flexuosa* from multiple LGM refugia. No paleoecological or phylogeographical studies are available from earlier glacial cycles, which prevents an evidence-based answer to this question.

It could be hypothesized that repeated contraction–expansion cycles might have led to greater genetic differentiation, possibly at the species level (for example, *M. flexuosa* and *M. carana*). For this to have occurred, glacial refugia would need to have remained relatively stable over time and space. For example, in Europe and North America, recurrent contraction–expansion cycles followed a north–south pattern, with refugial areas for thermophilous taxa concentrated in the southern peninsulas (Hewitt, 2000). In contrast, in the Neotropics, no geographical patterns have yet been established for the glacial–interglacial dynamics of lowland taxa, due to the lack of pre-LGM empirical data.

Paleoclimates

In many Neotropical paleoecological and phylogeographical studies, glacial aridity and postglacial wetting are often assumed without supporting paleoclimatic evidence. Similarly, glacial cooling and the subsequent postglacial warming are largely overlooked. To assess the potential effect of these climatic drivers on *Mauritia* dynamics, independent paleoclimatic evidence is needed.

Estimates based on noble gas concentrations in groundwater indicate that the Neotropics cooled by about 5°C during the LGM (Stute et al., 1995; Bush et al., 2001). Given a typical temperature lapse rate of –0.55 to –0.60 °C per 100 m in elevation—common in Amazonia and adjacent mountain regions (Zink & Huber, 2011; Rapp & Silman, 2012; Kirkels et al., 2020)—this cooling implies a downward shift of roughly 800–900 meters in the upper elevation limit of *Mauritia*. Such a shift would have compressed suitable habitat for this palm into a narrow band between sea level and 100–200 meters, likely leading to a major range contraction into isolated refugia (warm refugia), as reflected in pollen data (Fig. 2). Notably, the few LGM sites where *Mauritia* pollen has been found are all located below 300 meters, reinforcing this interpretation.

Regarding hydroclimates, oxygen isotope records from speleothems indicate a general precipitation reduction of about 60% during the LGM compared to present, with an east (drier)–west (wetter) dipole across Amazonia (Cheng et al., 2013). However, carbon isotope analyses by Wang et al. (2013) showed that this drying was insufficient to fragment lowland rainforests into a sea of C_4-dominated grasses, as proposed by the classical RH. Even if some forest fragmentation did occur, *Mauritia* could likely have persisted and thrived, as this palm grows in a variety of biomes and ecosystems with drier and more seasonal climates than those required for lowland rainforests (e.g., Urrego et al., 2011, 2016; Rosa et al., 2013; Rull & Montoya, 2014; Mendes et al., 2017; Sander et al., 2022; de Ávila et al., 2023; Hergoualc'h et al., 2024). Furthermore, *Mauritia* populations often establish in areas where lowland forests have been reduced by drought or fire (Urrego, 1997; Montoya & Rull, 2011) (Fig. 3). Consequently, forest contraction and savanna expansion might have facilitated *Mauritia*'s spread across savannas rather than led to a decline in its range—a pattern that runs counter to the paleoecological evidence (Fig. 2).

Figure 3. *M. flexuosa* palm stands (´morichales") from the Gran Sabana region (Venezuela). A) Extensive morichales in a deforested valley bottom. B) Dense morichal along a small savanna river. C) Superficial fire inside a morichal burning only ground herbs and tree seedlings. D) Rainforest-savanna-morichal mosaic landscape where forest (at the background) is retreating while savanna and morichales are expanding due to selective burning. In this case, the savannas show evident signs of recent (dark-brown patches) and past (light-brown and green patches) fires. Photos V. Rull. Modified from Rull & Montoya (2014).

A corollary is that, even though *Mauritia* is a lowland element, its glacial and postglacial dynamics should not be uncritically equated with those of lowland rainforests as a whole. For this palm, cooling could have been a major driver for glacial retreat to lowland warm refugia/microrefugia, whether forested or not, provided that permanent o seasonal freshwater bodies were available (Fig. 3). This is consistent with the results of phylogeographic studies showing the genetic adaptation of *Mauritia* communities to swampy microhabitats, independently of macrobioclimatic differences (Melo et al., 2020). The scarcity of LGM pollen records noted above could be attributed to the limited presence of such aquatic microenvironments – where sediment accumulation and preservation are more likely to occur – below ~200 m elevation during the LGM.

Shelf refugia

Potential glacial refugia for *Mauritia* should not necessarily be restricted to current lowlands. It is well known that during LGM, the relative sea level (RSL) dropped by 130–134 m compared to its present situation (Lambeck et al., 2014; Spratt & Liesecki, 2016), exposing large portions of continental shelves worldwide. In the Neotropical Caribbean region, this resulted in the full exposure of the continental shelf, providing a vast new area—extending up to hundreds of km offshore from the present coastline—for the colonization of terrestrial ecosystems, especially by lowland biomes (Rull, 2025). For example, the ability of *M. flexuousa* to grow in back-mangrove communities flooded with freshwaters – sometimes as the dominant species or in monospecific stands – is well known (Rull, 2024). These and other shelf environments would have provided thermal and locally swampy conditions suitable for *Mauritia* development during the LGM.

In northern South America, an average sea-level drop of ~132 m would have exposed most of the continental shelf, which is particularly extensive (up to ~300 km offshore) in its northeastern sector, in front of the present Guianan and Brazilian coasts around the Amazon mouth (Fig. 1). This contrasts with the western coasts (Colombia, Ecuador and Peru), where the continental shelf is much narrower. In addition, the Andean range would have represented a major topographical barrier to the dispersal of lowland taxa toward these coasts. Consequently, the potential for *Mauritia* to migrate to continental shelf refugia or microrefugia during the LGM was greatest in the Atlantic sector—except for the easternmost part—of the northern South American shelf, and lowest along the Pacific coasts. In the northernmost region, represented by the Venezuelan Caribbean coasts, the continental shelf also contains relatively extensive areas; however, the presence of high coastal ranges would have hindered seaward migration. The same applies to the southeastern Brazilian coasts, where the shelf is well developed but coastal ranges would likewise have posed a barrier.

In summary, the most favorable shelf areas for LGM refugia of *Mauritia*, from which this palm could have expanded inland during postglacial times, were the northeastern Atlantic coasts around the Amazon mouth. Such eventual recolonization could have been facilitated by the Amazon river network, as rivers have been considered major dispersal agents for *Mauritia* (Sander et al., 2017).

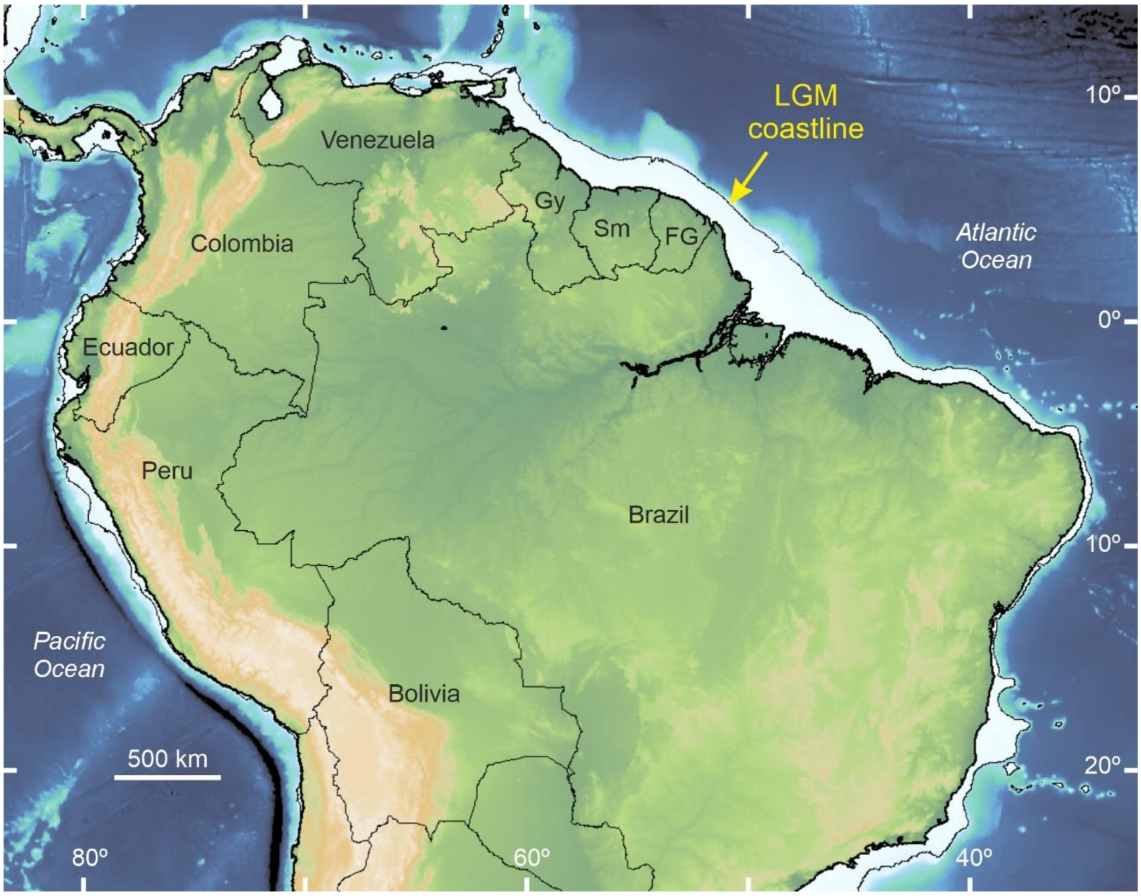

Figure 4. Map of tropical South America indicating the -132 m isobath (solid line), which marks the average LGM coastline and approximately coincides with the continental shelf break. The Andean range is represented in orange tones. Map generated with GeoMapApp version 3.7.5 (https://www.geomapapp.org/, last accessed 21 Aug 2025) using the Global Multiresolution Topography (GMRT) synthesis (Ryan et al., 2009). FG, French Guiana; Gy, Guyana, Sm, Surinam.

Summary and further work

The case of *M. flexuosa* seems to require elements from both the RH and the DVH to be properly understood. Thus, these two hypotheses about glacial–interglacial dynamics appear complementary rather than mutually exclusive. Empirical paleoecological, phylogeographic, paleoclimatic and eustatic evidence suggests that refugia may have existed, but cooling – rather than aridification – would have played a crucial role. These refugia would have been essentially warm and with flooded areas, which does not necessarily imply wet macroclimates. Preferred sites were likely close to sea level, up to 200-300 m elevation, including portions of the continental shelf, especially from the Atlantic coasts. Further postglacial expansion was a continuous process, driven primarily by Holocene warming, while moisture availability varied over time. The presence of flooded areas was also a critical factor. The genetic structure of *M. flexuosa* populations across Amazonia is consistent with this postglacial expansion after the LGM. However, the divergence between *M. flexuosa* and *M. carana* remains unexplained due to the lack of empirical data.

This empirically based approach provides a new framework for understanding glacial retraction and postglacial expansion of *Mauritia*, while circumventing the classical RH–DVH debate. It also offers insights into the types of studies needed to test the main hypotheses involved. From a paleoecological perspective, sedimentary sequences spanning several glacial–interglacial cycles are essential for reconstructing Pleistocene dynamics and assessing potential recurrent trends in *Mauritia* behavior, with emphasis on the specific locations of glacial refugia and postglacial expansion pathways. Within this framework, phylogeographical studies may shed light on speciation events and the emergence and eventual fixation of subspecific clades. Paleoclimatic records based on pollen-independent proxies from the same cores used for pollen analysis would be instrumental in reconstructing past local conditions, particularly moisture availability and flooding patterns. When planning new coring campaigns, consideration should also be given to the continental shelf, especially along the Atlantic coasts, to identify potential glacial refugia.

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