The Role of Quaternary Spatiotemporal Gradients and Dynamic Disequilibrium in Shaping Present Neotropical Biotic Patterns

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1. Introduction

The longstanding myth of tropical climatic stability and its influence in the shaping of low-latitude biogeographical and ecological patterns was definitively dismantled in the mid-late 20th century, when the first evidence of Quaternary glacial-interglacial climate shifts was documented, and the corresponding biogeographical responses were reconstructed. Damuth & Fairbridge (1970) documented the occurrence of arid conditions in Amazonia during the Last Glacial Maximum (LGM; ~21,000 years before present or ~21 ka BP). Working in the Amazon avifauna, Haffer (1969) proposed that LGM lowland forests would have been fragmented into isolated patches, or refugia, in a sea of savannas, thus favoring allopatric speciation by vicariance. From these refugia, the forests and the associated avifauna could have expanded during wetter interglacials, which would have promoted coalescence, thus favoring gene flow and hybridization by secondary contact. Similar results were obtained by Vanzolini & Williams (1970) for lizards. Later, Prance (1982), Whitmore & Prance (1987) and Haffer & Prance (2001) summarized the occurrence of similar situations in other organisms and identified the purported lowland refugia based on present rainfall patterns and current biodiversity distribution.

However, further palynological work failed to find evidence for LGM aridity (Colinvaux, 1987; Colinvaux et al., 1996) and supported the continuity of lowland rainforests, albeit with a different taxonomic composition. This change was attributed to the downward migration of montane species caused by cooling, moderate precipitation reduction, and atmospheric CO_2 depletion. This was called the disturbance-vicariance hypothesis or DVH (Bush, 1994). Therefore, the refuge hypothesis (RH) was not needed to explain the biogeographical patterns observed in the Neotropical lowlands (Colinvaux et al., 2000). Following Gentry (1982), proponents of the DVH emphasized the importance of the Andean uplift and the stability of Amazon forests during the Neogene in shaping current Neotropical biogeography (Colinvaux & De Oliveira, 2001). In this framework, Neotropical biotic patterns would have emerged during the Neogene, while the Quaternary would have been a time of range reorganization and possibly of extinction (see also Wesselingh et al., 2010). This view was not shared by other paleoecologists working in the Neotropics (van der Hammen & Hooghiemstra, 2000), who maintained Haffer's (1969) initial idea of wet refugia. The debate still persists and is centered on hydroclimatic patterns.

The advent of molecular DNA phylogenies revolutionized knowledge of Neotropical diversification, and the number of studies supporting either Neogene or

Quaternary diversification flourished. A first meta-analysis including a wide range of organisms showed that extant Neotropical species originated continually from at least the Miocene (>20 Ma) until the Pleistocene, with no diversification bursts at any time period (Rull, 2008). Nearly half of the analyzed species were Neogene in origin, while the other half emerged during the Pleistocene. Similar results were obtained by Turchetto-Zolet et al. (2013) for a wide range of South American species. Therefore, it was proposed that the dual Neogene-Quaternary controversy did not make sense and that current Neotropical biotic patterns resulted from a complex interplay of ecological and evolutionary processes across spatial and temporal scales, initiated by Neogene tectonics and continued under the action of Pleistocene climatic changes (Rull, 2011a, b). Examples of the spatiotemporal complexity of the origin and evolution of Neotropical biodiversity can be found in Hoorn & Wesselingh (2010), Hoorn et al. (2010), Antonelli et al. (2015, 2018), and Rull & Carnaval (2020), among others.

This paper focuses on the Quaternary, particularly the last glacial cycle, from the LGM onward. This cycle serves as a general model for the approximately 40 Pleistocene glacial-interglacial cycles, which follow similar trends, albeit with variations in intensity and duration (Raymo, 1994). The target areas are tropical South America, especially the Amazon/Orinoco lowlands, the Caribbean coasts, and the Guiana Highlands (Fig. 1). Extensive paleoclimatic and paleoecological records from both terrestrial (e.g., the Bogotá Basin) and marine (e.g., the Cariaco Basin) settings (see Fig. 1) demonstrate that Neotropical biomes and ecosystems were affected by glacial-interglacial cyclicity throughout the entire Pleistocene (e.g., Hooghiemstra, 1984; Haug et al., 1998; Yarincik & Murray, 2000; Torres et al., 2013). Unfortunately, similar records are unavailable for most Neotropical areas, including those studied here, where the last glacial cycle is widely represented and has been studied in more detail.

The main aim of this chapter is to analyze key spatiotemporal biotic gradients driven by Quaternary environmental shifts. In this context, the primary objective is to show how environmental forcing—mainly climatic changes and sea-level shifts—created varying conditions for evolutionary, biogeographical, and ecological interactions that have shaped current biomes and ecosystems. These observations are also discussed from the perspective of the equilibrium dynamics of biotas and ecosystems under environmental forcing. The target areas and taxa (mostly vascular plants) selected for study were chosen to represent a diverse range of settings (coastal, lowland, montane), biomes (mangroves, rainforests, savannas, high-mountain regions), and ecological requirements (climate, topography, flooding, salinity tolerance) in order to assess the different biotic responses to environmental drivers. Another selection criterion was the author's own experience in the subject matter, which has inevitably led to extensive self-citation, although this has been substantially reduced.

2. An Iconic Neotropical Palm

Mauritia flexuosa is one of the most abundant and widely distributed palms across the Neotropics, with an estimated 1.5 billion individuals (ter Steege et al., 2013). It can thrive in a variety of vegetation types—such as rainforests, gallery forests, savannas, forest-savanna mosaics and coastal forests—either as a forest component or in monospecific stands (Fig. 2). This lowland palm requires warm and wet climates and grows from nearly sea level to approximately 1000 m in elevation, usually in soils flooded by freshwater (e.g., riverbanks, lake shores, valley bottoms and coastal marshes), as it is salinity-intolerant (Vegas-Vilarrúbia et al., 2007). *M. flexuosa* has multiple uses for humans and has been part of indigenous cultures for a long time. Some of these cultures refer to *M.*

flexuosa as the “tree of life.” Fruits are the most valued resource, but almost every part of the palm is used for food, housing, ornamentation, fiber extraction, medicine or rituals, among many other purposes. More details on *M. flexuosa* and its human uses can be found in Rull & Montoya (2014) and Virapongse et al. (2017).

According to Bogotá-Ángel et al. (2021), the ancestors of *Mauritia* originated in Africa during the Cretaceous and expanded into South America and India during the Paleocene. The global cooling associated with the Eocene-Oligocene transition (EOT) led to the extinction of *Mauritia* in India and a significant reduction in its diversity in Africa, where it became extinct during the Oligocene. Therefore, *Mauritia* has been restricted to the Neotropics since the Miocene. Presently, *M. flexuosa* grows in the northern South American lowlands of the Orinoco, Amazon and adjacent basins, between approximately 12°N and 24°S (Fig. 3).

Over 40 sites within the current *M. flexuosa* distribution range, situated at elevations from near sea level to 1040 m, have been cored to reconstruct Late Pleistocene–Holocene vegetation trends from pollen records (Fig. 4). The oldest record, dating from shortly before the LGM, shows *Mauritia* pollen at a few localities, with two sites near 20°S exhibiting significant abundances. During the LGM, this pollen was still present at the same sites, but the percentages dropped to less than 1% at all of them. In the Lateglacial, the distribution expanded longitudinally, and slight recovery in pollen percentages was observed in some localities. Both the expansion and the population recovery accelerated during the rapid Early Holocene global warming (EHW) and a regional increase in precipitation (Haug et al., 2001). The expansion reached its maximum in the Middle Holocene, during the Holocene thermal maximum (HTM), coinciding with a precipitation peak. In the Late Holocene, the abundance of *Mauritia* increased in the northwestern sector under stable temperatures, despite a significant regional drying trend (Haug et al., 2001). The role of humans as dispersal agents, especially during the last 2 ka, should not be disregarded. Human influence may have been manifested through active or passive fruit transport as well as through selective burning of forests and savannas, thereby favoring *Mauritia* expansion (Rull & Montoya, 2014).

The whole picture is consistent with postglacial expansion from scattered lowland LGM refugia (or microrefugia; Rull, 2009), where *Mauritia* could have survived the last glaciation. While the biogeographical pattern appears to support the RH, the environmental drivers behind glacial retraction and subsequent postglacial expansion remain unclear. Similar results were obtained in a study in eastern Amazonia that combined molecular phylogeography, niche modelling, and paleoecological records. According to de Lima et al. (2014), extant *M. flexuosa* exhibited low global genetic diversity but significant genetic differentiation among populations from different river basins. This was interpreted as evidence of range retraction into refugia during the LGM and attributed to increased aridity, in line with the classical Neotropical RH. The authors attributed the LGM aridity to latitudinal shifts of the Intertropical Convergence Zone (ITCZ), but no paleoclimatic data were provided regarding the magnitude of the aridity shift.

Independent paleoclimatic data indicate that tropical South America was significantly colder and drier during the LGM than it is today. Indeed, previous studies using noble gases dissolved in groundwater have pointed to an overall cooling of approximately 5°C compared to present-day temperatures (Stute et al., 1995). In contrast, paleoprecipitation patterns estimated from oxygen isotope records in speleothems were more heterogeneous, reflecting an east–west dipole—with relatively stable, wetter climates in western Amazonia and more unstable, drier conditions in the east (Cheng et al., 2013). Estimated precipitation was reduced by nearly 60% compared to modern levels, yet this decrease was insufficient to transform forests into savannas dominated by C_4 grasses, as indicated by carbon isotope analysis (Wang et al., 2013). How might this reduction in precipitation have affected *M. flexuosa*?

First of all, it is important to stress that *M. flexuosa* grows in a variety of biomes and ecosystems, including open savannas characterized by drier, more seasonal climates than those required for lowland rainforest development. Therefore, if the aridity shift did not exceed the forest threshold, as suggested by Wang et al. (2013), it is expected that *Mauritia* would be less affected. Moreover, even in the case of hypothetical forest fragmentation within a savanna landscape, as proposed by the RH, this should not have posed a problem for *M. flexuosa*, since the species thrives in savanna environments (Fig. 2) as well as in vegetation mosaics that include forests, savannas and “cerrados” (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* stands typically replace lowland forests when these experience reductions due to dryness or fire (Urrego, 1997; Montoya & Rull, 2011). Therefore, forest reduction and savanna expansion may even favor *Mauritia* expansion rather than shrink its range.

In contrast, cooling during the LGM could have been more influential. Considering a temperature lapse rate of -0.55 to -0.60 °C per 100 m in elevation—which is typical in Amazonia and the surrounding mountain slopes (Zink & Huber, 2011; Rapp & Silman, 2012; Kirkels et al., 2020)—a temperature drop of approximately 5°C could correspond to a lowering of 800–900 m in the upper limit of *Mauritia*. This could have significantly reduced the habitat suitable for this taxon to a narrow elevation range between sea level and 100–200 m, likely causing a severe range reduction in *Mauritia* and possibly fragmentation into refugia, as observed in pollen records (Fig. 4). Therefore, the primary environmental constraint for this taxon during the LGM would not have been moisture availability, but low temperatures.

In summary, the reduction of *M. flexuosa* during the LGM, as evidenced by paleoecological records, does not conform to the classical view of extended Neotropical aridity with wet refugia. Rather, it appears to be primarily a case of general cooling that led to the formation of warm refugia and/or microrefugia. This RH framework is not incompatible with, but rather complementary to, the DVH involving the downward migration of montane species into the Neotropical lowlands and the corresponding changes in forest taxonomic composition. The rapid Holocene expansion coinciding with the EHW and the subsequent stabilization during the HTM, along with the western expansion despite Late Holocene regional drying (Haug et al., 2001), supports the thermal refuge hypothesis for *Mauritia*. This explanation is also compatible with the evolutionary history of the subtribe Mauritiinae, to which *Mauritia* belongs, which was primarily influenced by cooling events (Bogotá-Ángel et al., 2021).

3. The Caribbean Mangroves

Mangroves are forested ecosystems found in tropical and subtropical intertidal zones, playing a crucial role in preserving coastal biodiversity and providing essential ecological services. They are also among the most significant blue-carbon ecosystems, contributing to global warming mitigation. Mangroves grow around the average sea level, forming zonal vegetation gradients from low to high tides and transitioning from saline to oligohaline or freshwater environments. They thrive particularly in flat sedimentary terrains but are absent on steep coastal slopes, rocky shores, or littoral cliffs. Typical mangrove elevations range from -1 m to 3.5 m, extending from a few hundred meters to several kilometers inland, with average slopes between 0.01% and 0.45% (Ellison et al., 2024). Mangrove ecosystems are structured around a limited number of dominant tree species—known as mangrove-forming trees—which possess specialized morphological and physiological adaptations to saline environments (Tomlinson, 2016).

In the Caribbean region, mangroves cover approximately 14,700 km², accounting for about 10% of the world's mangrove surface (Bunting et al., 2022) (Fig. 5). The main mangrove-forming trees in the region include the red mangrove (*Rhizophora*, Rhizophoraceae), black mangrove (*Avicennia*, Acanthaceae) and white mangrove (*Laguncularia*, Combretaceae). Additional components, such as the tea mangrove (*Pelliciera*, Tetrameristaceae) and the mangrove fern (*Acrostichum*, Pteridaceae), are also common but typically occupy marginal environments. Caribbean mangroves first emerged during the Middle Eocene, initially dominated by *Pelliciera*. However, during the Eocene-Oligocene Transition (EOT), *Rhizophora* became the dominant mangrove-forming tree. The Neogene period saw increased diversification, ultimately shaping the present-day mangrove composition. During the Quaternary, Pleistocene glacial-interglacial cycles and human activities further influenced Caribbean mangrove ecosystems. A detailed account of their evolutionary history is available in Rull (2024a).

Quaternary records of Caribbean mangroves correspond mostly to the Holocene, with only a few Late Pleistocene records dated to approximately 130 ka BP and 70–30 ka BP (Mitchell et al., 2001; González et al., 2008; González & Dupont, 2009). The Last Glacial Maximum (LGM) remains undocumented, and the earliest postglacial records date to ~12 ka BP (Pocknall & Jarzen, 2024). Considering the LGM global relative sea level (RSL) drop of 130–134 m below present levels (Lambeck et al., 2014; Spratt & Liesecki, 2016), the entire Caribbean continental shelf would have been exposed (Fig. 6), severely reducing the flat areas (FAs) suitable for mangrove growth. It has been proposed that, under these conditions, Caribbean mangroves may have survived in restricted flat refugia or microrefugia beyond the shelf break. However, the lack of paleoecological records from this period hinders testing of this hypothesis.

A preliminary approach to the problem involved a microtopographical bathymetric image analysis using the Global Multi-Resolution Topography (GMRT) tool (Ryan et al., 2009). The main objective was to identify the most suitable prospects for flat areas (FAs) around -132 m (the average LGM-RSL drop) that could have potentially supported mangrove growth during the LGM. Using the global elevation averages cited above (Ellison et al., 2024), the analyzed depth range was -128 to -133 m, with prospective slope ranges between 0.01% and 0.45%. Applying these parameters, a detailed examination of shelf break topography along the entire Caribbean coastline identified zones with a higher probability of containing FAs suitable for mangrove growth. Further high-resolution analysis of topographical profiles within these areas pinpointed the most promising prospects for mangrove development (Rull, 2025).

The results of this analysis indicate that during the LGM, much of the Caribbean coastline was unsuitable for mangrove growth, leaving only a few FAs where these ecosystems could have persisted. The most substantial concentration of mangroves was likely located on the northern Trinidad (NT) shelf, which may be considered the main mangrove refugium during the LGM, along with the Cariaco Basin (CB) (Fig. 6). Additional suitable locations consisted of small, kilometer-scale dispersed areas that could have served as microrefugia for mangroves (Fig. 6). A high-resolution analysis of the largest and most suitable NT potential refugium is presented as an example (Fig. 7). In this area, the most prospective FAs lie in the central sector and decrease toward the east and west, where the coastline becomes steeper. This is illustrated by a central land-sea elevation profile (NTC), where the potential mangrove boundaries span nearly 6 km inland with an average slope of 0.09%. An example of an unfavorable topographical gradient is found on the western side (NTW), where the horizontal space for mangrove growth is less than 200 m, with an average slope of 3.05%. A range of intermediate conditions exists across the NT site, including slopes close to the upper limit, as shown in an eastern profile (NTE) with an average slope of 0.41%.

The location of the main potential refugial areas (NT and CB) suggests that as sea levels rose after the LGM, mangroves likely expanded across the Caribbean coastline, with their primary sources of recolonization being refugia and microrefugia situated in the southeastern region. It is known that surface coastal currents are the main agents responsible for dispersing mangrove propagules (van der Stocken et al., 2019). In the Caribbean, the primary surface currents enter through the eastern coasts via the Northern Equatorial Current (NEC) and the Guyana Current (GC), flowing through the Lesser Antilles and northern Trinidad, respectively, before entering the Gulf of Mexico via the Yucatán Channel (Fig. 5). As this circulation pattern has remained constant since the LGM (Rull, 2025), surface circulation would have favored westward mangrove expansion from the primary NT and CB refugial areas across the Caribbean, with minor contributions from other microrefugia. These preliminary results should be validated through further coring campaigns in the identified potential refugia and microrefugia to confirm the actual occurrence of mangroves during the LGM.

Again, this is an unconventional approach to the RH in the Neotropics, with sea-level drop, rather than climate, as the primary environmental driver. Climatic shifts may also have played a role, but with the available evidence, it is not possible to determine to what extent. A remaining enigma is the type of vegetation that occupied the exposed shelf during the LGM. Considering the cooling mentioned above, it would be reasonable to assume that the most temperature-sensitive lowland species—and possibly those with high thermal tolerance—could have migrated downward and colonized the newly exposed shelf space for terrestrial biota. One such species could have been *Mauritia flexuosa*. Once again, the RH and the downward DVH appear to be complementary rather than opposing explanations. However, paleoecological records to confirm this point remain unavailable. Much paleoecological work is still needed on the Caribbean continental shelf. Such an initiative could benefit from existing paleoecological and paleoclimatic studies in similar tropical mangrove-bearing environments with emerged continental shelves during the LGM, notably the Indo-Malayan Sundaland shelf (review in Huang et al., 2024).

4. The Pantepui Oscillator

The Pantepui biogeographical province, situated atop the Guiana Highlands (GH) (Fig. 1), is one of the few remaining pristine areas in the world due to its remoteness and inaccessibility. Topographically, Pantepui consists of an assemblage of more or less flat summits of approximately 70 table mountains—the tepuis—ranging in size from less than 1 km² to 1000 km², with a total area exceeding 5000 km², situated at elevations between 1200/1500 and 3000 m (Fig. 8). It has been described as an archipelago of "sky islands" and is frequently referred to as a "lost world," a term popularized by Arthur Conan Doyle’s novel *The Lost World*, which was inspired by the GH landscape and its remoteness. The pristine nature of Pantepui makes this province a unique natural laboratory for studying the origin and evolution of Neotropical biodiversity under natural conditions, free from direct human influence (Rull, 2010). The uniqueness, biodiversity, and endemism of Pantepui organisms and their communities are remarkable. Plants are by far the most diverse group (~2600 known species), while amphibians have the highest percentage of endemic species (55%), with other groups generally ranging from 30% to

40%. The Pantepui ecosystems are unparalleled in other Neotropical regions. See Rull et al. (2019) and Rull & Vegas-Vilarrúbia (2020) for an updated account of Pantepui life and environmental features.

As usual, the current Pantepui biota is the result of a long ecological and evolutionary history, although in this case, most inferences come from present biogeographical patterns. This is due to the absence of sediments between the Precambrian and the Quaternary, as well as the scarcity of available molecular phylogenetic and phylogeographic studies, largely due to the difficulty of obtaining fieldwork permits (Rull & Vegas-Vilarrúbia, 2008). In summary, the different hypotheses proposed to explain the origin and evolution of the Pantepui biota can be reduced to the classical biogeographical debate between vicariance and dispersal (review by Rull, 2019). Regarding the Quaternary, the RH has also been applied to the GH. Based on biodiversity and endemism patterns of vascular plants, Steyermark (1979) proposed that Pantepui as a whole could have served as a wet refugium during the LGM. However, the lack of pre-Holocene peats suggests that LGM climates atop the tepuis were arid, which contradicts the proposed Pantepui wet refugium hypothesis (Schubert & Fritz, 1995; Schubert et al., 1994).

Further paleoecological studies demonstrated that several temperature-sensitive Pantepui species migrated upward and downward in response to warmer and cooler climates, respectively, during the Holocene (Rull, 2004a, b; Rull & Montoya, 2017). This confirmed previous insights based on the current range of medium-elevation Pantepui species (Steyermark & Dunsterville, 1980) and suggested that the vertical displacement during the LGM would have been greater. Further studies conducted immediately south of Pantepui recorded the presence of elements from tepuian montane forests—e.g., *Podocarpus*, *Hedyosmum*, *Wenmannia*, *Alnus*—in the surrounding lowlands during the LGM. This was consistent with a 1000-1100 m downward displacement of these sensitive species and a 5-6°C temperature drop, as recorded by independent methods for the Amazonian lowlands (Bush et al., 2004). Therefore, an approximate average downward migration potential of 1100 m, characteristic of the Neotropics (Farrera et al., 1999), was adopted for Pantepui thermal-sensitive species.

Once in the lowlands, these species not only altered lowland forest composition but also dispersed horizontally and eventually climbed to other tepuis during postglacial times (Fig. 9). Other species, situated more than 1100 m higher than the surrounding lowlands or uplands, would have been “trapped” on the tepui summits, unable to reach the lowlands. It has been estimated that more than 70% of the vascular flora would have been able to move among the tepui summits (Rull & Nogué, 2007). In this way, both vicariance and gene flow played a role in the diversification of the Pantepui biota during the Pleistocene (Rull, 2005).

This view aligns more closely with the DVH and suggests that the Pantepui biota, as well as that of the surrounding lowlands and uplands, may have varied significantly throughout the Quaternary. Additionally, total annual rainfall in Pantepui ranges from 2500 to more than 3500 mm (Zink & Huber, 2011), and even a highly unlikely 60% decrease—similar to that estimated for Neotropical lowlands during the LGM (Wang et al., 2013)—would still be insufficient to induce arid conditions, as previously proposed by Schubert et al. (1994). The key enigma is the biota that occupied the tepui summits during glacial phases, as no elevations above 3000 m were available from which species could have migrated downward. It has been suggested that glacial summits may have supported species with high temperature tolerance, other unknown species now extinct—the so-called "glacial ghosts" (Rull, 2007)—and possibly Andean species capable of crossing the Orinoco Basin during glacial cooling events (Rull et al., 2019). Similar LGM teleconnections have been proposed for several Andean forest genera known to occur in the Brazilian Atlantic Forest (Pinaya et al., 2024) (Fig. 1). To address this novel dynamic perspective of Pantepui, a model called the Pantepui Oscillator (PO) was proposed. This model should be regarded as a hypothesis to be tested in the future through paleoecological studies—provided that Pleistocene sediments do exist and are eventually discovered atop the tepuis.

The PO dynamic model is based on a fixed element—topography—and two shifting components: climate and biota (Rull & Vegas-Vilarrúbia, 2019). In the present-day Pantepui, these three elements coincide, as this biogeographical province was defined based on current topography, climate and biota. However, during a glaciation, these three components become disassembled: the topographic Pantepui remains, while the other two migrate downward (Fig. 10). This migration, however, differs between the climatic and biotic Pantepui. Whereas the climatic Pantepui shifts downward in a relatively uniform manner, following the temperature lapse rate, the species of the biotic Pantepui migrate at different rates, depending on their specific thermal requirements and the availability of topographic corridors. The same pattern applies to their upward migration during interglacial periods. This process creates a complex and dynamic spatiotemporal scenario that, repeated approximately 40 times across ~70 tepuis and their surrounding lands, has shaped the present-day Pantepui biota. A key implication is that the current Pantepui may be just one of approximately 40 Pantepuis that have existed throughout the Quaternary, due to the idiosyncratic responses of different species to glacial-interglacial shifts of varying intensity and duration.

5. Disequilibrium Dynamics

It is not unusual to perceive the current interglacial period in which we live as the "normal" state of biomes and ecosystems, while glacial conditions are seen as transient bottlenecks that species must endure to avoid extinction. In this view, the *Mauritia* warm refugia, mangrove topographical refugia and disassembled Pantepui may be regarded as unstable conditions that will eventually equilibrate in the next interglacial. However, the Quaternary is actually a glacial period during which the Earth has been glaciated 80% of the time (Willis & Whittaker, 2000). Therefore, glaciations, rather than interglacials, can be considered the norm (Bush et al., 2001). Moreover, a thermodynamic perspective challenges our perception of glacial versus interglacial equilibrium dynamics.

Although glacial-interglacial cycles are governed by symmetrical, astronomically driven solar cycles of energy input to the Earth—i.e., the Milankovitch cycles (Berger, 1988)—paleotemperature records from ice cores exhibit a characteristic asymmetry between glacials and interglacials. Whereas interglacial warmings are short and abrupt events, glacial coolings follow a gradual and extended trend (Fig. 11). Interglacial warmings occur at the end of glaciations and proceed at faster rates than insolation increases. This acceleration is driven by magnification factors, such as changes in albedo and atmospheric CO_2 concentration, which amplify the climatic system's response to solar forcing (Ellis & Palmer, 2016). Consequently, interglacials are triggered by abrupt inputs of additional energy into the climate system, and when these inputs cease, the system gradually returns to its glacial state.

In simple thermodynamic terms (Hill, 1960), interglacials represent short, unstable states driven by external energy inputs, while glacials correspond to the system's gradual relaxation toward maximum entropy levels once external energy input ceases. Thus, the Quaternary may be viewed as a period characterized by a long-term stable glacial climate, periodically interrupted by short and abrupt unstable interglacial warmings (Bush et al., 2001). Returning to the examples discussed above, warm refugia for *Mauritia*, topographic refugia for mangroves and Pantepui disassembly may be considered the stable states, whereas *Mauritia* and mangrove expansion, along with Pantepui coupling, would represent transient and unstable states—potentially to be stabilized, or not, in the next glaciation.

This situation is consistent with the concept of nonequilibrium dynamics introduced by Hutchinson (1957), who argued that competitive exclusion—leading to the extinction of most species and the dominance of one or a few—requires a stable environment. In contrast, even small, short-lived environmental changes can alter competitive relationships, thereby contributing to spatiotemporal niche segregation and promoting diversification. Davis (1981) used paleoecological evidence to support this idea in the postglacial expansion of North American forests. According to her, constant environmental variations at diverse spatial and temporal scales lead to dynamic disequilibrium (or nonequilibrium dynamics), in which plant communities are continuously modified without ever reaching equilibrium. The Quaternary shifts of *Mauritia*, Caribbean mangroves and Pantepui, among many others, could serve as examples of this concept. However, contrary to common perception, interglacials would represent external disturbances, while glacials would serve as the stabilizing phases.

6. Current Global Warming and Sea-Level Rise

In the examples discussed here, temperature and eustatic shifts have been identified as the primary drivers of biogeographical and ecological change. Therefore, it could be asked what the future holds for *Mauritia*, the Caribbean mangroves and Pantepui in a warming world with rising sea levels. Many models suggest that the interglacial period in which we currently live, the Holocene, will last longer than usual due to ongoing anthropogenic global warming.

Some models predict that the next glaciation could be delayed by 40,000 years (Herrero et al., 2014). Others suggest that rising atmospheric CO_2 concentrations will override the influence of astronomical solar cycles—the primary drivers of glacial-interglacial cyclicity—disrupting this cycle for at least a million years (Haqq-Misra, 2014). A third, more extreme set of predictions warns of a point-of-no-return, beyond which glacial-interglacial cycles would cease indefinitely, leading to a permanent “hothouse” Earth. This scenario would be characterized by high global temperatures with minimal latitudinal differences, ice-free poles, and significantly higher sea levels. Steffen et al. (2018) proposed that a mere 2°C rise above preindustrial temperatures could trigger a cascade of positive feedback loops, ultimately resulting in a hothouse Earth. At least 15 such hothouse phases, lasting several million years, have been documented in Earth's history (Kidder & Worsley, 2014). The most recent occurred in the Early Eocene, when global temperatures were approximately 16°C higher than today and relative sea levels were about 60 meters above present levels (Miller et al., 2020; Westerhold et al., 2020).

For *Mauritia*, rising temperatures and a reduced thermal latitudinal gradient could allow it to colonize higher elevations, likely in the Andes and the GH slopes, and expand its latitudinal range. However, the extent of this expansion would depend on the niche characteristics of other species and *Mauritia*'s ecological relationships with them. In any case, *Mauritia* could benefit from global warming, provided that hydroclimatic conditions remain suitable for sustaining its preferred freshwater-flooded habitats. Fossil data indicate that Mauritiinae have been restricted to tropical regions since their Cretaceous origin, with no evidence of latitudinal expansion—even during past hothouse Earth states

(Bogotá-Ángel et al., 2021). Therefore, past analogues for a potential future expansion are lacking.

Mangroves could also benefit from a warmer Earth with higher sea levels. However, land topography and the predicted increase in meteorological hazards—particularly tropical cyclones and hurricanes, which are the most destructive forces affecting mangroves (Burgess, 2018)—would act as limiting factors, at least on a local scale. Unlike *Mauritia* and its phylogenetic relatives, fossil pollen evidence indicates that mangroves experienced global expansion during the Early Eocene under hothouse conditions. At that time, the northern boundary of mangroves, which is currently around ~30°N, extended as far as 80°N, near the deglaciated North Pole (Popescu et al., 2021).

In the case of Pantepui, the situation is different, as interglacial periods are associated with increased extinction due to habitat loss on mountaintops (Rull, 2005). Cold-adapted species are unable to migrate upward during warming events because there is no available terrain above 3000 meters. The flat topography of the tepui summits promotes biodiversity accumulation and supports larger populations than more conical mountains. As a result, biodiversity loss due to habitat reduction would be significantly greater atop the tepuis. Estimates suggest that 75–83% of Pantepui’s vascular flora could become extinct due to habitat loss by the end of this century, based on IPCC temperature projections for the region (Nogué et al., 2009). Of these, 28–54% are endemic species, meaning their extinction would be global. Additionally, it has been estimated that a temperature increase of 9°C—common under hothouse conditions—would be sufficient to drive the total extinction of Pantepui’s vascular flora (Rull & Vegas-Vilarrúbia, 2006). This would not only eradicate all vascular plants in Pantepui but also lead to the extinction of all species dependent on them for survival.

7. Synthesis and Further Work

The three examples discussed here illustrate LGM vegetation trends and patterns across two spatial (elevation and longitude) and two temporal (climate and sea-level shifts) environmental gradients. The elevation gradient extends from the depths of the Caribbean continental shelf (-132 m) to the summit of the Guiana Highlands (~3000 m), while the longitudinal gradient spans from western to eastern Amazonia. The temporal gradients encompass the transition from LGM cooling in tropical South America and the Caribbean lowstand to the Holocene warming and rising sea levels. Vegetation dynamics along these gradients also shaped biogeographic and ecological spatiotemporal patterns, driven by the idiosyncratic responses of species to environmental change. Together, these factors define a complex scenario of environmental forcing and biotic responses within a framework of disequilibrium dynamics, which has played a crucial role in shaping modern ecosystems.

Low LGM temperatures and sea levels led to downward biotic displacements, including mountain species migrating to the lowlands, lowland species like *Mauritia* seeking refuge near sea level—possibly on the exposed continental shelf—and mangroves retreating to a few refugia or microrefugia, primarily along the southeastern Caribbean shelf break. The ecosystems that occupied the highest elevations of the Guiana Highlands and the Caribbean continental shelf during the LGM remain unknown, and some of them have likely gone extinct, leaving behind "glacial ghosts." Overall, the biogeographical ranges of sensitive species were depressed, altering the composition of lowland forests and increasing discontinuities in certain taxa and ecosystems, particularly in *Mauritia* and mangroves.

Postglacial warming and sea-level rise favored the expansion of *Mauritia* and mangroves, along with the upward displacement of sensitive species to the mountains, altering the composition of lowland and slope forests. Dispersal across the lowlands during the LGM likely facilitated taxonomic interchange and gene flow among tepuis, while subsequent warming may have driven the extinction of sensitive high-elevation LGM species due to habitat loss. This would have significantly changed the composition of the Pantepui biogeographical province as it is currently defined. Additionally, glacial-interglacial variability and the resulting increase in diversification may have caused Pantepui to act as a "biodiversity pump" for the surrounding lowlands (Rull, 2005).

The recurrence of glacial-interglacial cycles throughout the Pleistocene has shaped modern biomes and ecosystems. However, these cycles have not been identical, as they have varied not only in extent and intensity (Raymo, 1994) but also in biotic reorganizations and disequilibrium dynamics in environmental-biotic relationships. As mentioned, ecological reorganizations resulted from species' idiosyncratic responses to environmental shifts, combined with lowland migrations across extensive areas, such as the Orinoco and Amazon basins, during long glacial phases. Disequilibrium dynamics arose from glacial relaxation and entropy increase, driven by the need to reach a stable state following short-lived and unstable interglacial external energy inputs. Whether equilibrium is ultimately attained depends on the specific characteristics of each glacial-interglacial cycle and the species involved.

While the exact magnitude remains unknown, most models predict that the next glaciation could be delayed for a long time, ranging from tens of millennia to millions of years. Some suggest that glacial-interglacial cycles could be interrupted indefinitely. The persistence of a more or less permanent interglacial state would not result from changes in solar energy, as astronomical cyclicity is expected to remain unchanged, but rather from anthropogenically driven amplification feedbacks, particularly the increase in atmospheric greenhouse gas concentrations. In this scenario, mangroves could expand toward the polar regions, as they did during the latest Early Eocene hothouse state, while the entire Pantepui vascular flora, along with its dependent biota, may face extinction. The fate of *Mauritia* remains uncertain.

Many of the ideas and proposals discussed above require further testing through paleoclimatic and paleoecological studies, ideally using records that span the entire Pleistocene. As mentioned, some exceptionally long records have been retrieved in the Neotropics. In the Caribbean, the Cariaco records have been instrumental in inferring the main Pleistocene climatic and oceanographic features of the region (Haug et al., 1998; Yarincik & Murray, 2000). However, paleoecological mangrove records are limited to a short period before the LGM (González et al., 2008; González & Dupont, 2009). In addition to revisiting stored cores to assess whether they still contain material useful for paleoecological research, coring other potential refugial areas, such as the northern Trinidad shelf, is highly recommended.

The Bogotá record, which contains a complete Pleistocene sequence, has been instrumental in reconstructing the glacial-interglacial oscillations of the northern Andean forests and the highland páramos, providing an exceptional reference for the South American tropics (Hooghiemstra, 1984; Torres et al., 2013). Despite decades of paleoecological prospecting, similar records have not been found in other Neotropical mountain ranges, lowlands or uplands. However, continued efforts in this direction are worthwhile. For example, more than four decades ago, Schubert (1980), based on seismic profiles, proposed that the sediments of te Venezuelan Lake Valencia, at ~400 m elevation (Fig. 1), could contain a record spanning at least the last 520 ka in the uppermost 300 m. To date, only the first ~7 m, corresponding to the Holocene, have been cored and studied paleoecologically (Bradbury et al., 1981; Binford, 1982; Leyden, 1985).

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Figure captions

Figure 1. Study areas of this paper (yellow boxes) in the Neotropical context. AF, Brazilian Atlantic forests; BB, Bogotá basin; CB, Cariaco basin; GH, Guiana Highlands; LV, Lake Valencia.

Figure 2. Examples of *Mauritia flexuosa* from the Gran Sabana region (Venezuela). A) Light palm stands around a lake. B) Dense monospecific gallery forest surrounded by savanna vegetation. The different colors in savanna vegetation are due to different the stages of vegetation regeneration after frequent fires. Photos: V. Rull.

Figure 3. Present distribution of *Mauritia flexuosa*. Downloaded from the Global Biodiversity Information Facility (GBIF) (https://www.gbif.org/; last accessed Jan 28, 2025).

Figure 4. Map of northern South America showing the localities containing *Mauritia* pollen in their Late Pleistocene and Holocene sedimentary records. The coring sites are indicated in blue – see Rull & Montoya (2014) for details and references – and the *Mauritia* pollen percentages in red.

Figure 5. Map of the Caribbean mangroves (green patches), according to Bunting et al. (2022). Downloaded from NASA Landsat 5-TM (https://earthobservatory.nasa.gov/images/47427/mapping-mangroves-by-satellite). The refugial areas identified by the microtopographical analysis are represente as red dots and the superficial currents as blue arrows. Refugia/microrefugia: CB, Cariaco Basin; NC, northern Colombia; NT, northern Trinidad; WH, western Hispaniola. Currents; CC, Caribbean current; GC, Guyana current; NEC, northern Equatorial current.

Figure 6. GMRT map of the Caribbean seafloor indicating the -132 m isobath, representative of the LGM relative sea level position. Note that this isobath coincides with the shelf break, indicating that the whole continental shelf (light gray) was exposed during the LGM. The most prospective zones used in the microtopographical analysis are shown by yellow boxes. CB, Cariaco Basin; NC, northern Colombia; NT, northern Trinidad; WH, western Hispaniola.

Figure 7. Magnification of the northern Trinidad shelf break (NT) showing the isobaths between -128 and -133 m at meter resolution, and representative examples of LGM coastal profiles (yellow lines) from west to east. The space available for mangrove growth is highlighted by a thick green line in the below profiles. Note that the NTW profile is a steep coast unsuitable for mangrove growth, whereas the NTC and NTE profiles fall within the coastal slope suitable for mangrove development (0.01%.0.45%). Methodological details in Rull (2025). Abbreviations: AS, average slope; LGM-RSL, relative sea level during the Last Glacial Maximum; LML, lower mangrove limit (-133 m); UML, upper mangrove limit (-128 m).

Figure 8. Examples of tepuis and tepuian massifs. A) The Roraima massif viewed from the Venezuelan Gran Sabana (photo: V. Rull). B) The Roraima summit and upper cliffs (photo courtesy of Javier Mesa). C) The Upuigma tepui and the surrounding Gran Sabana uplands (photo: V. Rull). D) the Ilú-Tramén massif (photo: V. Rull). See Rull et al. (2019) for details.

Figure 9. Schematic representation of the diversification model in Pantepui consistent with the disturbance-vicariance model. The tepui summits are in dark red and the vertical migration of sensitive species is represented by brown arrows. Simplified from Rull (2005).

Figure 10. The Pantepui oscillator. The orographic (green, climatic (pink) and biotic (yellow) Pantepui components assemble during interglacials (like the current Holocene) and disassemble during glacials by differential downslope migration. Redrawn from Rull & Vegas-Vilarrúbia (2019).

Figure 11. Temperature anomalies (blue line) with respect to the present average (dotted line) during the last four glacial cycles as recorded in the Vostok ice core (Antarctica). Interglacials are highlighted by gray bands. Note that the onset of interglacial warmings are abrupt, whereas glaciations exhibit a gradual temperature decrease (red lines) spiked by minor interstadial events (IS). Modified from Petit et al. (1999).

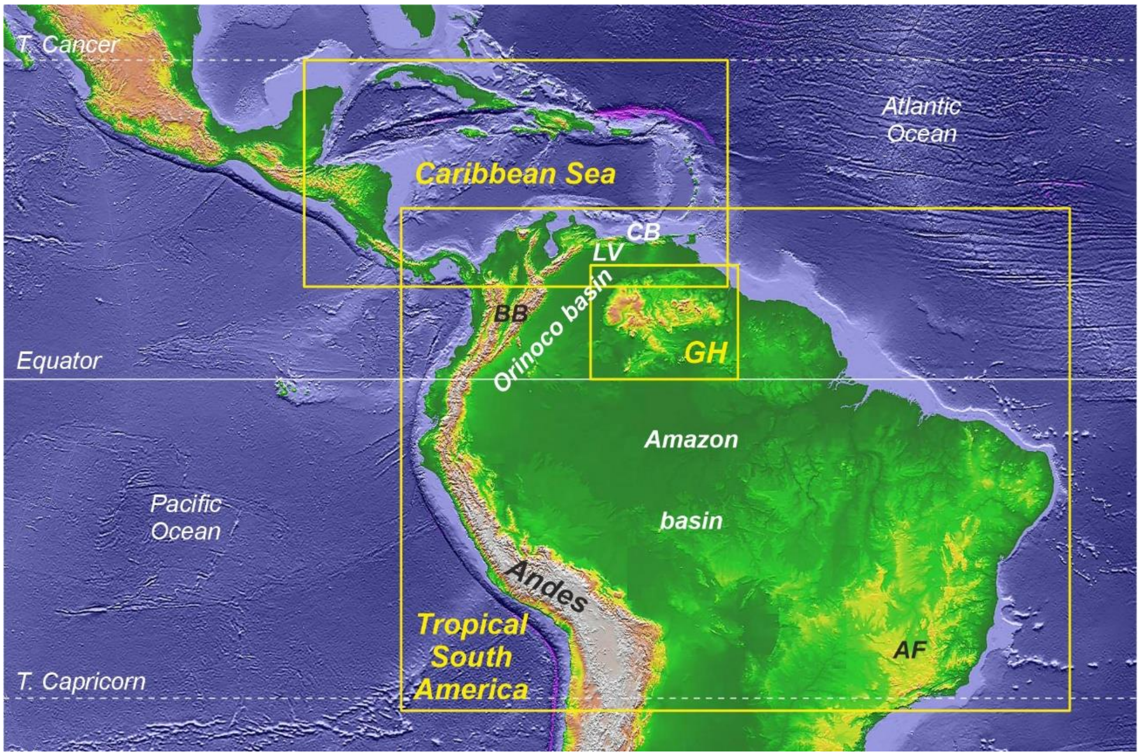

Figure 1

Figure 2

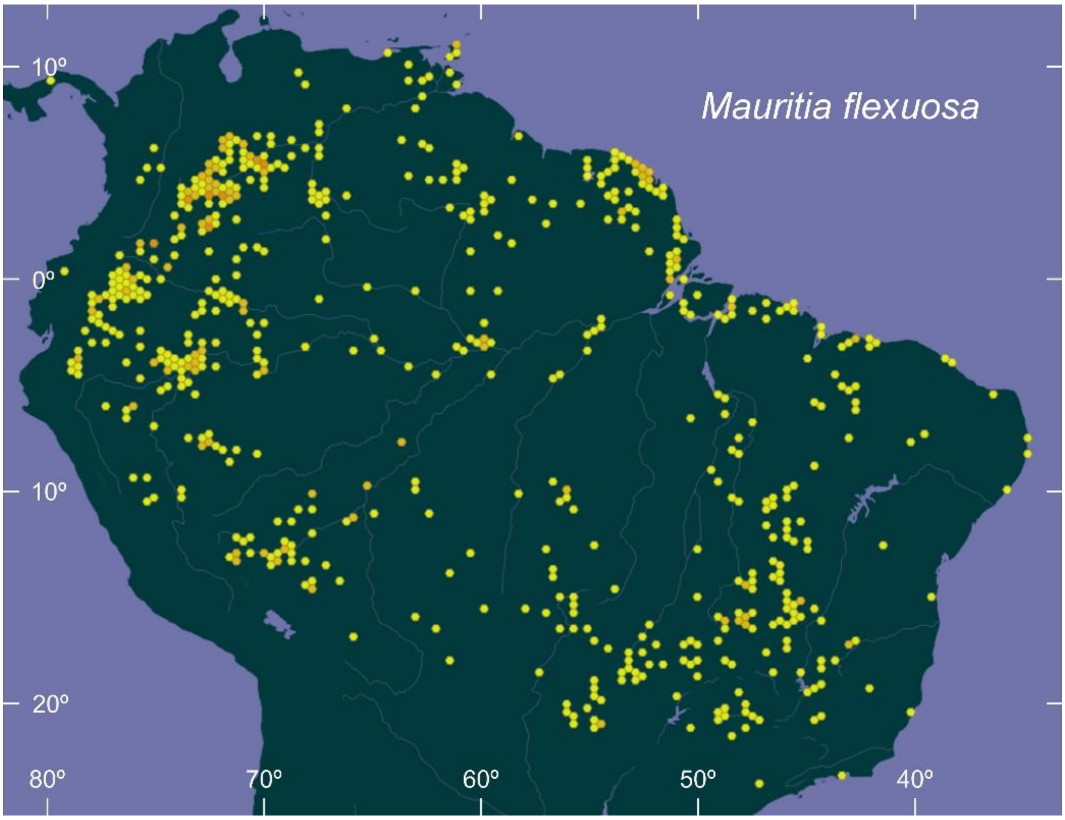

Figure 3

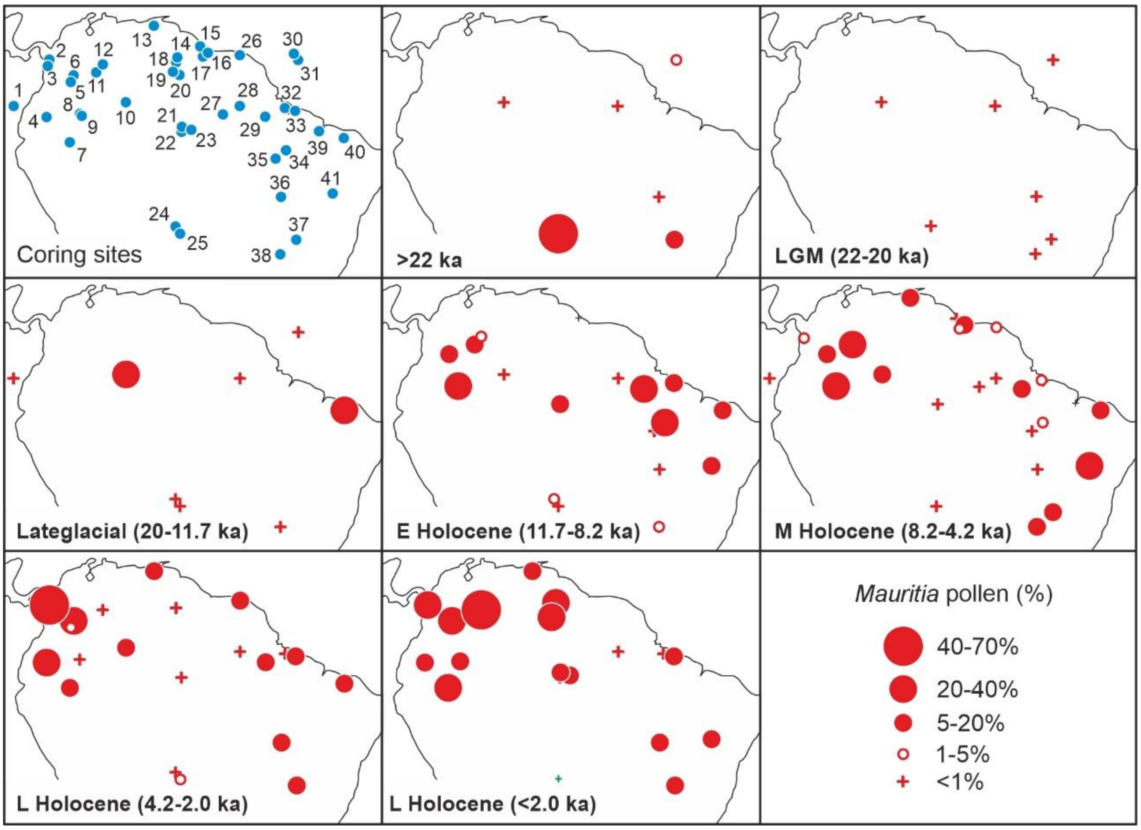

Figure 4

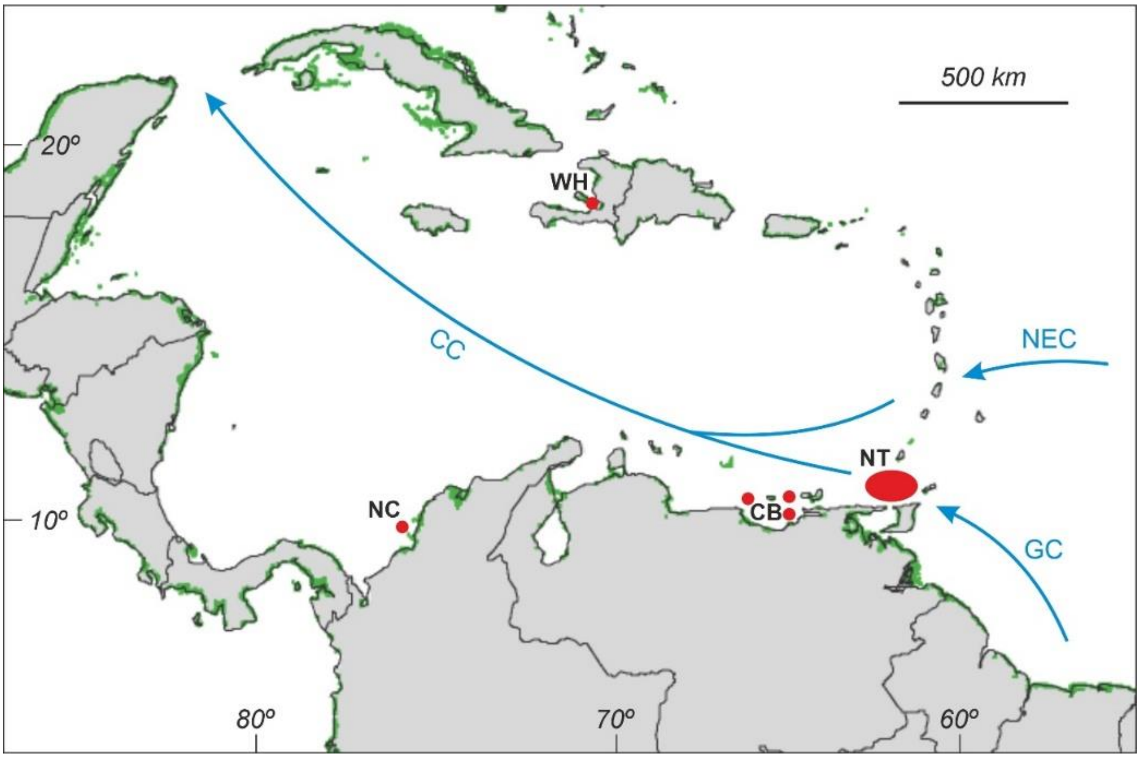

Figure 5

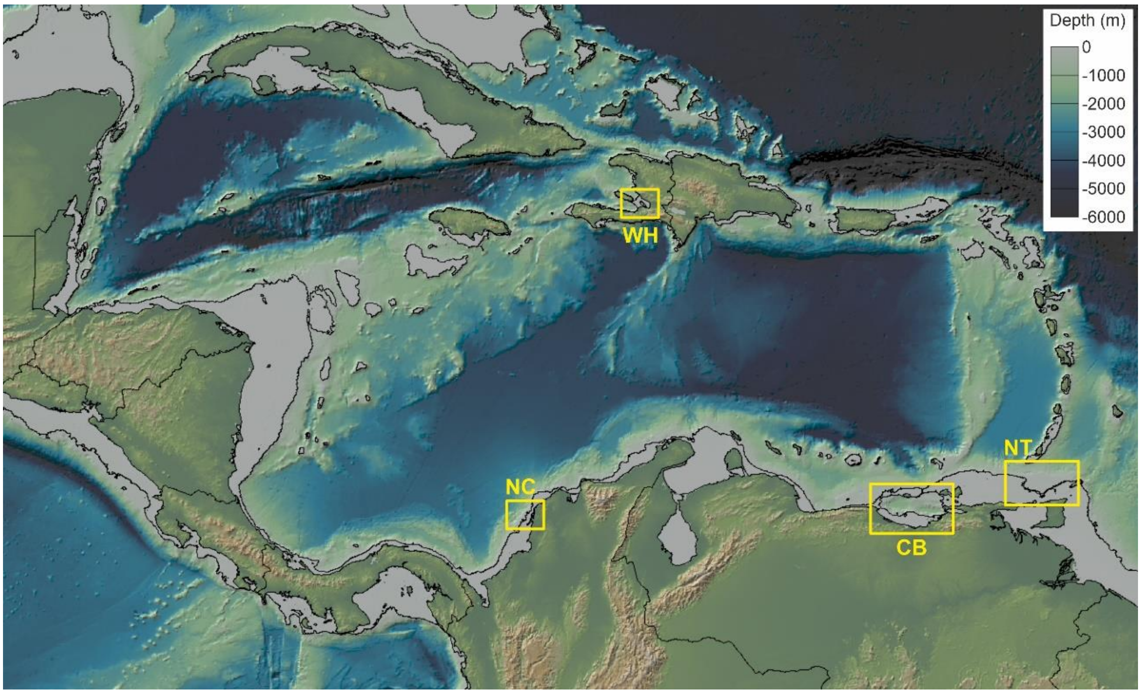

Figure 6

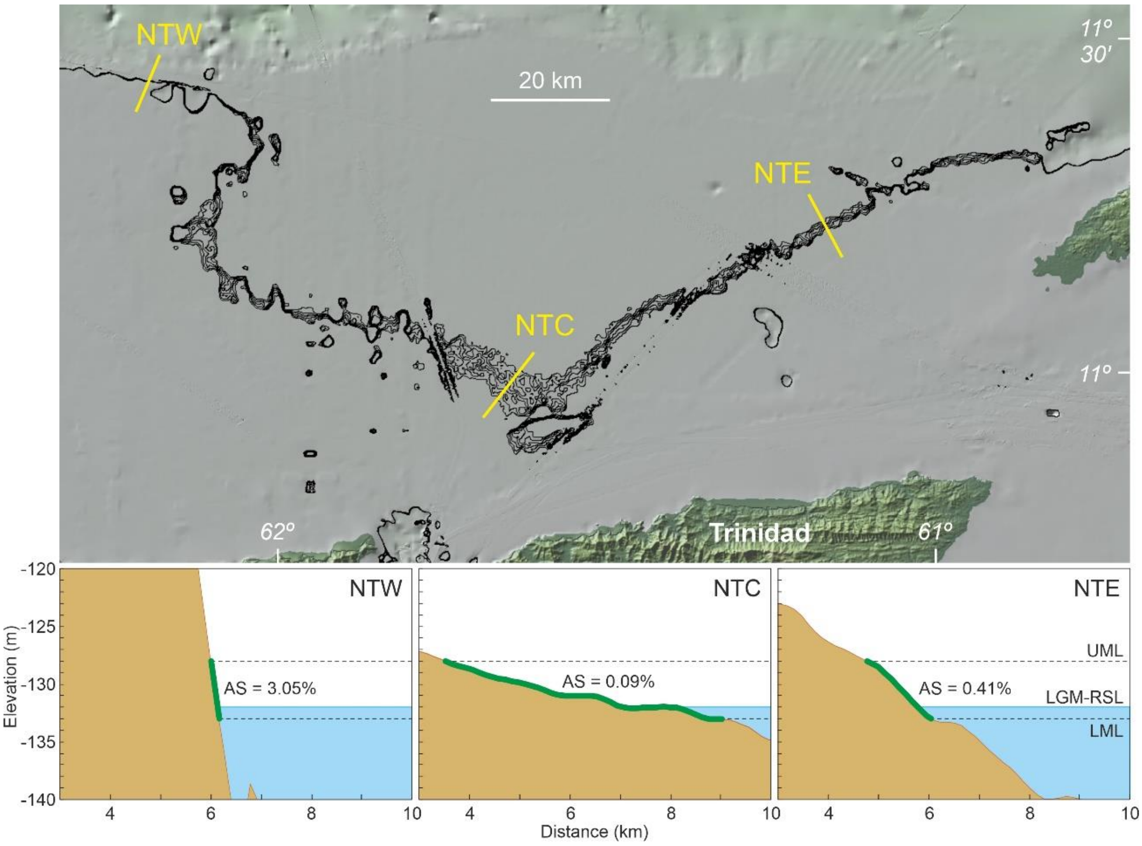

Figure 7

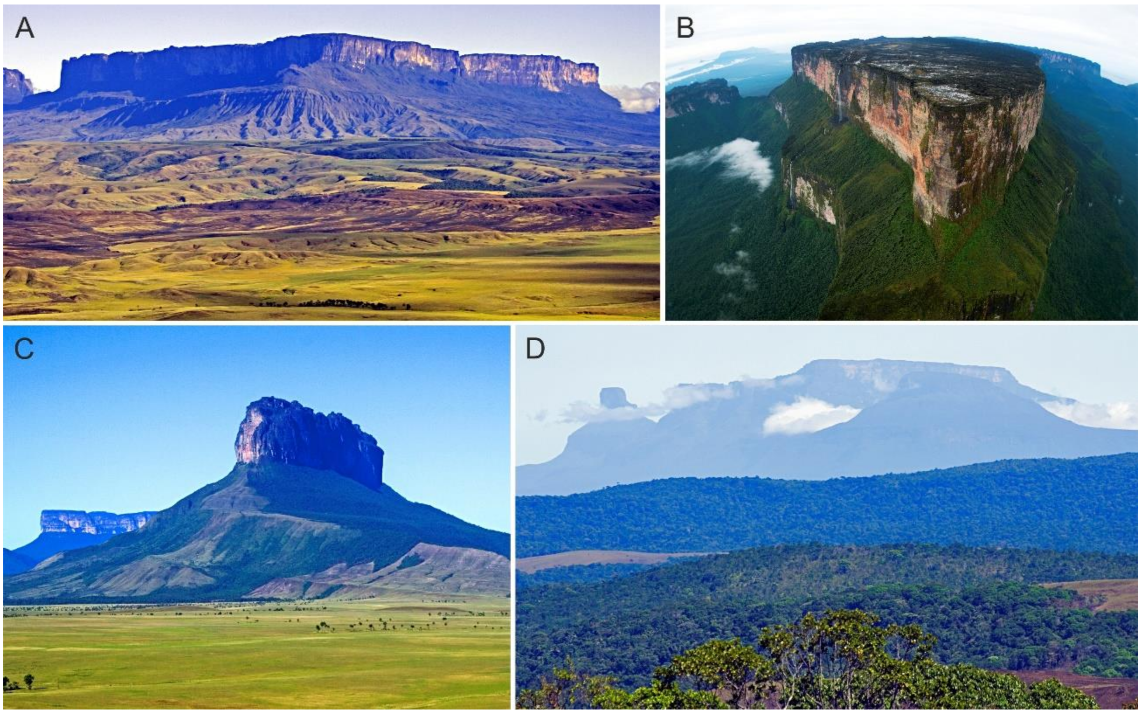

Figure 8

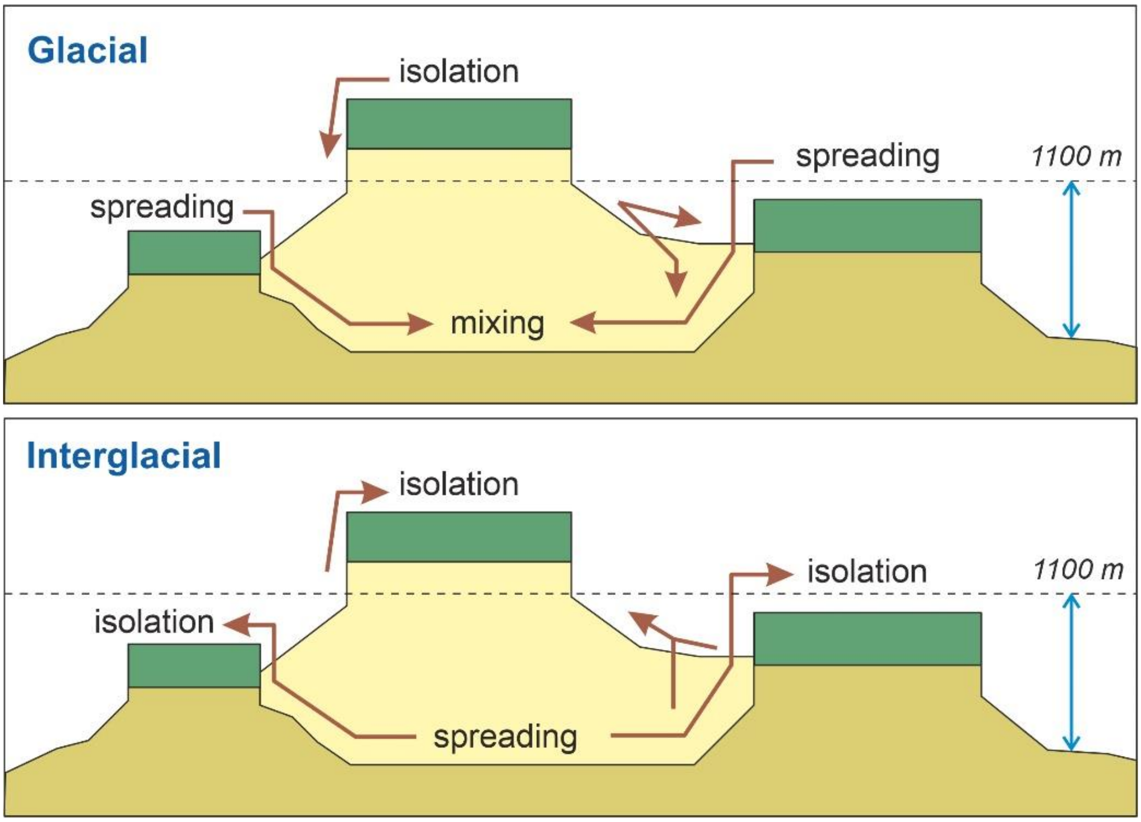

Figure 9

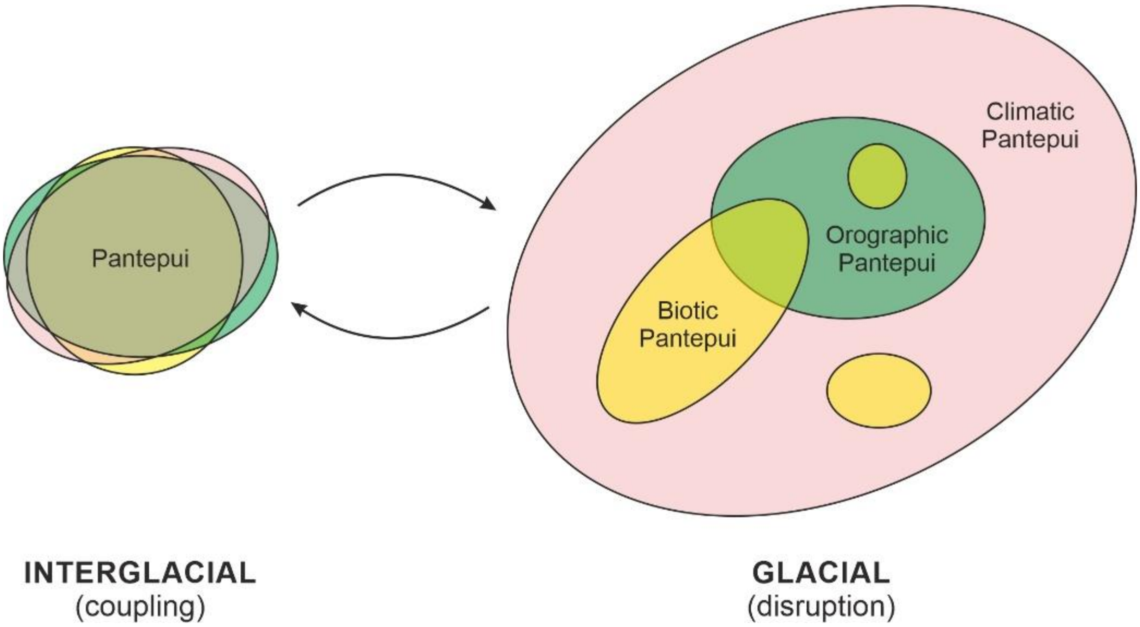

Figure 10

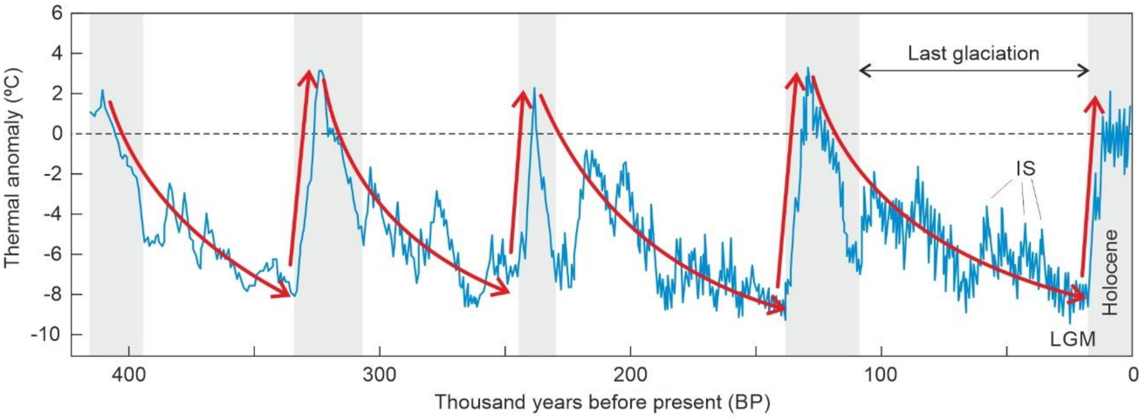
Thermal anomaly (ºC)
6
4
2
0
-2
-4
-6
-8
-10
400
300
200
100
0
Thousand years before present (BP)
Last glaciation
IS
LGM
Holocene

Figure 11