Beyond Refugia: New insights on Quaternary climate variation and the evolution of biotic diversity in tropical South America

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Abstract

Haffer’s (1969) Pleistocene refuge theory has prompted 50 years of investigation into the connections between climate, biome dynamics, and neotropical speciation. Although aspects of the original theory are not supported by subsequent studies, recent advances in paleoclimatology suggest the need for reevaluating the role of Quaternary climate on evolutionary history in tropical South America. In addition to the many repeated large-amplitude climate changes associated with glacial-interglacial stages (~100 kyr cyclicity), we highlight two less discussed causes of Quaternary climate change in South America: (1) an east-west precipitation dipole, induced by solar radiation changes associated with Earth’s precession about the sun (~20 kyr cyclicity); and (2) periods of anomalously high precipitation that persisted for centuries-to-millennia (return frequencies ~1500 yr) congruent with cold “Heinrich events” or cold Dansgaard-Oeschger “stadials” of the North Atlantic region. The spatial footprint of precipitation increase due to this North Atlantic forcing extended across almost all of tropical South America, south of the equator. Combined, these three climate modes present a picture of climate change with different spatial and temporal patterns than envisioned in the original Pleistocene refuge theory.

Responding to these climate changes, biomes expanded and contracted and alternately became connected and disjunct. Biome change undoubtedly influenced biotic diversification, but the nature of diversification likely was more complex than envisioned by the original Pleistocene refuge theory. In the lowlands, intermittent forest expansion and contraction led to species dispersal and subsequent isolation, promoting lineage diversification. These pulses of climate-driven biotic interchange profoundly altered the composition of regional species pools and triggered new evolutionary radiations. In the special case of the tropical Andean forests adjacent to the Amazon lowlands, new phylogenetic data provide abundant evidence for rapid biotic diversification during the Pleistocene. During warm interglacials and interstadials, lowland taxa dispersed upslope. Isolation in these disjunct climate refugia led to extinction for some taxa or speciation for others.
**Keywords:** refugia, tropical South America, Quaternary, paleoclimate, phylogenetics, geogenomics

**Introduction**

Publication of Haffer’s (1969) Pleistocene refuge theory encouraged researchers to seek connections between climate-biome dynamics and neotropical diversification. Based on centers of modern endemism identified for birds and lizards, Haffer (1969) and Vanzolini and Williams (1970) independently proposed that pulses of forest contraction and expansion in the Amazon basin, driven by Pleistocene glacial-interglacial climate cycles, forced population isolation and divergence, promoting allopatric speciation in forest refugia. This model assumed large-magnitude drying of the Amazon during the global ice ages that produced the contraction of wet tropical forest into isolated patches with replacement of intervening forest by vast expanses of savanna. In recent years, the Pleistocene refuge theory for Amazonia has been rejected by some who found little evidence either for significant Pleistocene aridity or for forest fragmentation (Colinvaux et al. 1996; Bush et al. 2004). The contention has also been made that crown-group ages in some groups of organisms date to the Neogene, in disagreement with the temporal framework of diversification implied in the Pleistocene refuge theory (Moritz et al. 2000; Hoorn et al. 2010). Yet phylogenetic studies across a wide range of plant and animal taxa increasingly point to the fact that many neotropical sister species did actually diverge in the Pleistocene (Richardson et al. 2001; Hughes and Eastwood 2006; Madriñan et al. 2013; Garzón-Orduña et al. 2014, Koenen et al. 2015; Byrne et al. 2016), opening the possibility of a role of Quaternary climate variation in the diversification of these biota (Rangel et al. 2018; Wheatley et al. 2019, but see Rull, Introduction to this volume and Vargas and Dick, chapter x).

In this contribution, we first review major advances in our knowledge of the nature of Quaternary paleoclimate variation at scales relevant to community compositional change and biotic diversification in tropical South America. We address if, and how, Quaternary climate variation affected forest distribution (Fig. 1) and composition, to the limited extent that we know either. Finally, we briefly present some phylogenetic evidence relevant to the question of how regional taxa may have evolved during, and in response to, periods of Quaternary climate change.

**Climate variability during the Quaternary**

*Was Amazonia drier during the Last Glacial Maximum (and other glacial intervals of the Quaternary) than it is today?*

We start our discussion of Quaternary climate variability by addressing the first question that has been oft revisited, but never definitively answered. Earth’s global climate was stunningly different only 20,000 years ago, at the Last Glacial Maximum (LGM), compared to today. Atmospheric CO₂ was reduced to ~180 ppmv; large ice sheets were present across boreal continental regions, particularly in North America; global eustatic sea level dropped 120 m below present; and global air temperatures averaged ca. 5°C colder than modern. In tropical South America, Andean snow lines lowered approximately 1 km and glacial erosion greatly increased the sediment load of Andean rivers and sediment delivery to inland basins (Fritz et al. 2007) and to the Atlantic Ocean. The Amazon continental shelf was exposed subaerially and
likely became vegetation covered (Leite et al. 2016), and the Amazon river incised its course for nearly 300 km across the shelf, delivering much of its sediment load to the Amazon deep-sea fan (Nace et al. 2014). These changes during the LGM (ca. 26,000 to 20,000 yr before present) were only the latest manifestation of some 50 prior glacial stages that occurred over the past 2.6 million years: lower-amplitude warm-cold cycles every 40 ky from 2.7 to ca. 0.8 Ma and higher-amplitude cycles every 100 ky since (Lisiecki and Raymo 2005).

A common and persistent misconception about Amazon paleoclimate is that the LGM (and earlier glacial stages) was drier than present throughout all of Amazonia. Whereas thermodynamics informs that ca. 35% less water vapor can be held in saturated air due to the ca. 5°C air temperature lowering deduced for the LGM in tropical South America (Stute et al. 1995), atmospheric dynamics can compensate for lower water vapor content by increasing lower-level winds bringing moisture from its Atlantic source into the Amazon. Such an increase could have been brought about both by a southward shift of the zonal mean position of the western Atlantic Inter-tropical Convergence Zone (ITCZ) during the LGM (Black et al. 1998; Peterson et al. 2000; Baker et al. 2001a) and the posited strengthening of the northeast Trades (McGee et al. 2018). Summer insolation over South America was at a maximum during the LGM and intensified the South American summer monsoon (SASM) (Baker et al. 2001; Cruz et al. 2005). Together, these three factors (ITCZ, trade winds, insolation) led to a generally high rate of precipitation, perhaps similar to modern, during the LGM in the SASM-region, i.e. the tropical central Andean region, the western Amazon, and subtropical South America. That conclusion is based on multiple lacustrine (e.g., Baker et al. 2001a, b; Baker and Fritz 2015) and speleothem (e.g., Cruz et al. 2005, Cheng et al. 2013) records of LGM climate from sites around the western and southern periphery of the Amazon (Fig. 2), from which we infer that western Amazon precipitation was high (i.e. comparable to modern) during the LGM.

Fewer paleoclimate records of the LGM exist from locations within the central and eastern parts of the Amazon basin and northeastern Brazil. Yet within the last decade, new speleothem records from northeastern Brazil (Cruz et al. 2009) and the eastern Amazon (Wang et al. 2017) indicate significant spatial variation of precipitation at orbital time scales across tropical South America. Specifically, Cruz and colleagues (2009) uncovered a precipitation dipole between the western Amazon/tropical central Andes and northeastern Brazil, varying with precessional (20 kyr) periodicity (Fig. 3). This finding was reinforced by a speleothem record from eastern Amazonia (Wang et al. 2017). Thus, in the western pole (western Amazonia, the tropical central Andes, the subtropics), precipitation increased during periods of increased summer insolation, while in the eastern pole (northeastern Brazil, the eastern Amazon), precipitation decreased during the same periods of higher summer insolation (Fig. 4).

The spatial footprint of this precipitation dipole is not well defined, because of the limited number of paleoclimate sites. Moreover, the longest speleothem record from the eastern dipole region (Wang et al. 2017) only extends back to 45,000 years before present. Although no terrestrial paleoclimate records that are presently available can confirm its long-term persistence, the existence of the east-west precipitation dipole is a robust feature of many different climate models forced by precessationally induced changes in insolation (Prado et al. 2013; Liu and Battisti 2015).

Wang et al. (2017) calculated on the basis of their speleothem isotopic record that precipitation during the LGM was 58% of modern in the eastern Amazon region, supporting the idea of a drier
eastern Amazonia at this time. However, they failed to adjust speleothem oxygen isotopic values for the estimated 5°C cooling at the LGM (Stute et al. 1995) and changes in seawater $\delta^{18}O$ (Schrag et al. 2002). When their speleothem record is corrected for these two effects (by subtracting ~2‰ from the LGM speleothem $\delta^{18}O$ value, see Baker and Fritz 2015), LGM $\delta^{18}O$ values nearly match modern $\delta^{18}O$ values in the same speleothem, from which we conclude that LGM precipitation was nearly equal to modern levels. Thus, precipitation in the eastern Amazon was similar to modern precipitation in that region, although relatively low compared to precipitation farther west. The corrected record indicates that it was the early-to-mid Holocene time period (~9000-5000 years before present) that had exceptional levels of precipitation. This period was evidently far wetter-than-modern in the eastern Amazon, while far drier-than-modern in the western Amazon (Punyasena et al. 2008) and tropical central Andes (Baker et al. 2001a; Cross et al. 2001).

In conclusion, data and models agree that there were large-amplitude fluctuations in precipitation amount on precessional time scales for the past 40,000 years in the near-equatorial regions, with drier conditions in the east accompanied by wetter conditions in the west, and vice versa. Furthermore, the models suggest that that this east-west precipitation dipole existed throughout the entire Quaternary and prior to that. However, the exact spatial footprint of the dipole, the magnitude of precipitation change, and its impact on the forest and associated biota, all remain to be determined. Whereas it is evident that spatially variable regions of climate change and forest expansion/contraction (Cheng et al. 2013) did not resemble the patterns envisioned by Haffer (1969), it is expected that climate-driven variation of forest biomes during the Quaternary had a profound influence on biotic dispersal, gene flow, and evolution.

**Short-term (millennial) extreme precipitation “events”**

Some of the intervals of most extreme precipitation change in tropical South America during the late Quaternary are not tied to gradual variations in insolation driven by orbital forcing, but instead were shorter-duration anomalies, persisting for one thousand to a few thousand years. This “millennial variability” is associated with large changes in sea surface temperatures in the North Atlantic region.

One example of such millennial variability, predominantly present during the last glacial stage, is Dansgaard-Oeschger (D-O) cyclicity. D-O cycles were first identified in the oxygen isotopic record of Greenland ice cores and determined to be warm-cold oscillations of air temperature (Dansgaard et al. 1993). Approximately 25 D-O cycles occurred between 10 and 90 Ka (Rahmstorf 2002). D-O cyclicity is also present in Antarctic ice cores (Steig and Alley 2002), where temperatures are anti-phased with Greenland (the “bipolar seesaw”) and amplitudes are of lower magnitude (see Pedro et al. 2018 and references therein). D-O cyclicity is recorded in sea-surface temperature proxies from North Atlantic sediment and widespread elsewhere in the Northern Hemisphere (Voelker et al. 2002). D-O cyclicity affected precipitation across the Neotropics: cold periods in the North Atlantic are associated with an apparent intensification of the SASM and increased precipitation everywhere in tropical South America south of the equator (Fritz et al. 2010; Kanner et al. 2012; Cheng et al. 2013; Wang et al. 2017), with the possible exception of the Pacific coast. How this persistent millennial variation during glacial stages impacted biotic communities in the heart of Amazonia remains to be addressed.
Heinrich events are a second type of millennial climate variability during glacial stages, closely related to D-O stadials (cold phases of the D-O cycles). Heinrich events appear to occur only during the most extreme D-O stadials. Heinrich events are characterized by the massive discharge of icebergs, primarily derived from the Laurentide Ice Sheet, into the North Atlantic Ocean (Broecker 1994). Subsequent melting of the icebergs significantly decreased sea-surface salinity of the North Atlantic, possibly shutting down the Atlantic meridional overturning circulation and increasing the abundance of sea ice in the North Atlantic. Although both the causes and the consequences of Heinrich events are still debated, there is no doubt that large-scale climate impacts, synchronous with the Heinrich events, were felt in many regions (Hemming 2004; Vellinga and Wood 2002). Paleoceanographic records from the Brazil continental margin (Arz et al. 1998; Nace et al. 2014) document large precipitation increases in northeastern Brazil synchronous with Heinrich events. On the Altiplano of Bolivia, Heinrich Event 1 (H1) brought about flooding and major expansion of now dry lakes (Sylvestre et al. 1999; Baker et al. 2001b). And Heinrich events coincide with the most negative δ18O values (indicating peak wet conditions) in speleothem records from the central Andes of Peru (Kanner et al. 2012) and the western Amazon (Mosblech et al. 2012; Cheng et al. 2013).

Thus, D-O stadials and Heinrich events had similar impacts on tropical South American climate (Fig. 5), although Heinrich events were apparently associated with more extreme climates than were the D-O stadials (Zhang et al. 2017), consistent with the fact that the former represented more extreme cold conditions in the North Atlantic region. Paleoclimate data show that wet climates associated with these North Atlantic cold events occurred simultaneously across all of tropical South America, south of the equator, in both eastern and western regions. Some of these wet events lasted as long as 5000 years (Nace et al. 2014), although most were shorter in duration. It seems likely that these North Atlantic warm-cold swings, associated respectively with large amplitude dry-wet swings in tropical South America, brought about profound changes in forest composition, extent, and biota.

**Biological responses to Quaternary climate variation**

*Biome expansions and contractions in response to orbital and millennial climate change. Was Pleistocene climate variability responsible for speciation?*

Paleoecological data compiled over the last few decades suggest that tropical forest composition was dynamic in response to changes in climate, but there remains little evidence of large-scale shifts in the geographic distribution of major Amazonian biomes on glacial to interglacial time scales as envisioned by Haffer (Bush et al. 2004). The apparent persistence of wet tropical forest in the central Amazon has major implications for phylogeographic studies of other organisms associated with forest settings. For instance, animal populations may have remained stable even in the case of temporal turnover of tree species, as long as the structural forest environment remained similar over time (Prates et al. 2016a). Yet, the paucity of sites in the heart of the present-day Amazon forest and of records that date back more than ~60,000 years means that we still have a very incomplete picture of spatial and temporal variability of regional biomes (Fig. 1). While the stability or instability of wet tropical forests in central Amazonia remains largely unsettled science, there is clear evidence of biome expansion and contraction near rainforest-savanna ecotones in the southern and eastern Amazon regions (Absy et al. 1991; Burbridge et al. 2004; Hermanowski et al. 2012; Reis et al. 2017).
Pollen data also suggest vegetation responses to the large wet millennial events of the late-Quaternary in regions marginal to, but outside of, Amazonia. In areas of northeastern Brazil now occupied by semi-arid Caatinga, humid gallery forests apparently expanded during Heinrich 1 and the Younger Dryas events (Behling et al. 2000; Ledru et al. 2006; Dupont et al. 2010; Bouimetarhan et al. 2018). This forest expansion may have been sufficiently extensive to have produced a landscape mosaic with wet forest corridors connecting the Atlantic and eastern Amazon forests (Cheng et al. 2013; Bouimetarhan et al. 2018).

Phylogenetic data suggest links between Quaternary climate variation and speciation. For example, a pattern of sister relationships between species and clades from Amazonia and the Atlantic Forest in several bird and small mammal groups (Costa 2003; Batalha-Filho et al. 2013) is consistent with the hypothesis that expansion of open and dry habitats (i.e., Caatinga dry forest and Cerrado savanna) following intervals of wet forest expansion favored speciation of rainforest organisms. In another example from the Atlantic Forest region, Carnaval and colleagues (Carnaval et al. 2009, 2014) tested whether vertebrate phylogenetic endemism was related to forest persistence over the last 120 Ka. Their analysis, using climate model output, suggests that forest stability was necessary but not sufficient for maintaining high levels of endemism. In addition, patterns of endemism differ between northern and southern regions of the Atlantic Forest, which apparently had divergent climate histories. This integration of geologic and genetic approaches (geogenomics, sensu Baker et al. 2014) provides a potentially powerful means of testing models of climatic, biotic, and evolutionary history.

**Shifts in community composition through climate-mediated dispersal**

Studies of diversification in Amazonian organisms have often emphasized in situ speciation, but the composition of local species pools is also strongly affected by migration between regions (Wiens 2004; Antonelli et al. 2018), and several examples of climate-mediated dispersal during the Quaternary have been proposed for Amazonia. For instance, a stepping-stone like corridor of dry vegetation formations may have favored migration of dry-adapted tree species (Bush 1994) and viperid snakes (Quijada-Mascareñas et al. 2007) through an otherwise wet forest matrix. Similarly, climate-driven geomorphic processes that affected the distribution of sandy soils may have created corridors for dispersal of dry-adapted taxa (D’Apolito et al. 2017); alternatively drier conditions may have permitted dispersal of white sand forest specialists within a former non-analog forest matrix (Capurucho et al. 2013). The patchy distribution and low species endemism of the physiognomically distinctive white sand flora across the Amazon basin (Adeney et al 2016) support the latter idea. In addition, pollen records suggest that cold-adapted upland taxa (e.g. *Podocarpus*) descended to the lowlands and expanded through the Amazon forest in response to past climate cooling (Colinvaux et al. 1996), creating assemblages that have no modern analog (Bush et al. 2004; Reis et al., 2017). This kind of migration, followed by subsequent extinction within a wetter Amazon, could explain plant disjunctions between the Guiana Shield and Andean slopes (Berry and Riina 2005).

Climate-driven opportunities for dispersal may have produced large-scale biogeographic interactions between Amazonia and other South American biomes, with pronounced effects on the composition of regional assemblages. For instance, reconstructions of population history on the basis of genetic data from arboreal lizards point to the establishment of rainforest corridors connecting eastern Amazonia with the northern Atlantic Forest in northeastern Brazil during the mid-Pleistocene (Prates et al. 2016a, b). This finding is consistent with reconstructed pulses of
increased precipitation on the basis of speleothem records, as discussed above (Cheng et al. 2013). Thus, climate-driven habitat shifts may have affected biotic composition and associated gene pools in Amazonia and adjacent regions by favoring not only speciation but also dispersal.

Perspectives on Climate, Topography, Soils and Diversification in the Quaternary

As with all other proposed mechanisms for speciation, it is difficult to conclusively demonstrate a direct link between Pleistocene climatic cycles and speciation. Instead, we are resigned to demonstrate a correlation between the recent timing of speciation for many taxa and the known large-amplitude variability of Pleistocene climate. As we have reviewed in this paper, recent paleoclimate studies firmly establish that large-amplitude Pleistocene climate variability did extend into the Amazon basin and the tropical Andes. And many important groups of rain forest and Andean taxa did diversify during the Pleistocene (e.g., Richardson et al. 2001; Kay et al. 2005; Hughes and Eastwood 2006; Lavin 2006; Erkens et al. 2007; Pouchon et al. 2018).

Pleistocene climate variability superimposed upon pre-existing Andean topography provides a perfectly plausible, not novel (e.g., Wiens, 2004), mechanism for driving speciation in high relief terranes. It has long been observed (Gentry 1982) and recently modeled (Rangel et al. 2018; Wheatley et al. 2019) that much of the taxonomic diversification of tropical South America has arisen in the tropical Andes. Although Neogene and earlier history may explain some of this diversity (Luebert and Wiegend 2014; Antonelli et al. 2009), much Andean diversification certainly is recent and therefore may be associated with Quaternary climate dynamics (van der Hammen and Cleef 1986; Madriñán et al. 2013). Under interglacial or interstadial warm conditions, montane forest and alpine taxa colonize upslope, where populations may be disjunct from each other because of topographic isolation—valleys form genetic barriers whose effective porosity is related to their width and depth. Subsequent cooling can reconnect isolated populations as they disperse downhill, encouraging genetic exchange between formerly disjunct populations, but also introducing newly divergent species back into the lowlands. Mountain tops thus serve as real climate refugia promoting allopatric speciation boosted by biotic interactions and ecological divergence (Lagomarsino et al. 2016, Vargas and Simpson, in review).

The Andes are only the most extreme of the mountains that circumscribe the Amazon. Lower-elevation ranges, such as the Guianan tablelands and Roraima to the north, the Serra do Divisor to the west, the Serra dos Gradaus and Serra do Cachimbo to the south, virtually surround the central Amazon basin. Pleistocene climate variability is known to have strongly impacted the biota of at least some of these regions (e.g., Reis et al. 2017) and new species may have arisen in these regions by a mechanism similar to that in the Andes. Novel taxa originating around the margins, may have dispersed downward and inward, producing high-diversity biota of mixed origins in the central Amazon. While there is compelling evidence linking rapid speciation and Pleistocene climate in the Andes, and plausibly for the circum-Amazon ranges, generalizations for the origins of Amazon-centered plant taxa are largely speculative. Climate variability can bring about biome expansions and contractions could hypothetically take place in lowland forests, for example, when dry conditions permit drought-adapted tree species within Amazon sand-soil forests or seasonally dry forests to expand from their habitat islands only to become re-isolated during wetter periods.

Another important layer for a revised Pleistocene refuge theory is incorporation of the influence of geological substrate and soils. For example, although it has been posited that seasonally dry
forests are currently restricted into their “refugia” and were more broadly distributed during the LGM (Pennington et al. 2000), the absence of rich, high pH soils between contemporary dry forests would have hindered their broad expansion. Although the distribution of soils has been poorly mapped in the Andes-Amazon region, the functional response of the tree canopy to spatially-varying substrate has been resolved at local scales and mapped over large biogeographic areas (Asner et al. 2015), providing new tools for assessing potential edaphic and nutrient influences on biodiversity and its origins.

For some taxa, Pleistocene diversification follows upon a longer evolutionary trajectory that was surely influenced by Neogene mountain uplift or long-distance dispersal (Richardson et al., 2001; Erkens et al., 2007) and pre-Pleistocene climate variability. Acceptance of Pleistocene climate as a likely driving influence for speciation in many taxonomic groups across the neotropics does not exclude the role of other speciation mechanisms, such as ecological divergence, as suggested by edaphic-dependent turnover in floral composition (Tuomisto et al. 2016, Asner et al. 2015), habitat specialization (Fine et al. 2014), and biotic interactions (Dobzhanski 1967; Kay et al. 2005). In fact, studies of diversification in lowland trees, such as neotropical Lecythidaceae (Vargas and Dick 2019) and Protiae (Fine et al. 2014), report similar speciation rates in the Pleistocene as prior to the Pleistocene, suggesting that Pleistocene climate variation affected taxa differently depending on their elevational gradient, generational time, and biotic interactions posing interesting questions for future research.

Our revised understanding of climate variability also may help to explain why so many tree species in the Amazon are rare—if their current populations represent a decline in abundance from past periods with more favorable climates. Periodic mixing and population changes associated with spatio-temporal climate variability may also explain why Amazon tree communities are widely dispersed and appear to have little community phylogenetic structure (Dexter et al. 2017). Climate variability would also help to explain how drought-tolerant and drought-intolerant species come to reside in the same forests, and it is predictive of which categories of species are most likely to persist through anthropogenic drought conditions (Esquivel-Muelbert et al. 2019).

Conclusions

Although Haffer (1969) posited large climate and biome variation during the Quaternary, at the time of his publication he could not marshal supporting paleoclimatic or paleobiotic information. Paleoclimatic studies during the intervening decades have fully established that there was very large, extrinsically forced, coherent, climate variation during the Quaternary across the Amazon, northeastern Brazil, subtropical Brazil, and the tropical Andes. It is now clear that the Amazon basin as a whole was not uniformly drier-than-modern during Pleistocene glacial intervals. Instead, the western Amazon, the central Andes, and the southeastern sub-tropics were similarly wet as at present during the Last Glacial Maximum (for example), whereas the eastern Amazon/northeast Brazil region was similarly dry as today. Past wet and dry intervals of the Quaternary occurred on both orbital and millennial timescales, and the spatial footprints of wet and dry regions also varied, both east-west and north-south. In particular, large precipitation and effective moisture increases occurred coherently on millennial timescales across all of tropical South America, south of the equator, concurrent with cold “Heinrich events” and D-O stadials of the North Atlantic region. In short, Quaternary climate variation was neither monolithic nor
necessarily contemporaneous solely with global glacial-interglacial cycles; rather the pacing and spatial footprint of past climates varied on both orbital and sub-orbital timescales.

Genetic evidence from a range of taxa is consistent with the hypothesis that alternately wet and dry conditions during the Quaternary respectively brought about forest expansion, with connection between the eastern Amazon and eastern Atlantic rain forests, and forest contraction with separation of the two forested regions into “mega-refugia” separated by non-forested Cerrado or Caatinga biomes. Yet, not every forest contraction produced effective vicariance for forest-dwelling biota; this may require longer-duration or more severe dry periods, and it must also have a stochastic element. Genetic evidence also reveals that the regions of high topographic relief surrounding the central Amazon lowlands, were site of explosive radiation associated with Quaternary cold-warm cycles and events. These regions may have served as species pumps, enriching the diversity of the intervening lowlands.

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Figure Legends

Figure 1. Biome map adapted from Olson et al. (2001; BioScience 51, 933–938) with their tropical ecoregions reclassified into tropical montane forest, rain forest, savanna, and dry forest biomes. Because of scale, small areas of some biomes embedded within other biomes (e.g., isolated savannas in Amazonia, patches of dry forest within Brazilian savannas) cannot be depicted. Modified from Pennington et al. (2018).

Figure 2. Location of sites discussed in the text. See Table 1 for site key and additional site details.

Figure 3. Sketch of the temporal evolution of precipitation of the eastern and western Amazon through one precession cycle.

Figure 4. A map of the east to west precipitation dipole in tropical South America on precession time scales (20 kyr) that shows the difference in DJF precipitation (mm d⁻¹) observed between low summer insolation (218 Ka) and high summer insolation (207 Ka) experiments. From Liu and Battisti 2015.

Figure 5. A sketch of the impact of millennial cold and warm variability in the North Atlantic region on the position of the ITCZ and trade winds and on precipitation throughout tropical South America. See text for additional details.
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<th>Site #</th>
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<th>Record</th>
<th>Proxies</th>
<th>Reference</th>
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<th>Long °W</th>
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<td>9</td>
<td>Groundwater</td>
<td>Maranhao, Brazil</td>
<td>noble gas</td>
<td>Stute et al. 1995</td>
<td>7 °S</td>
<td>41.5</td>
<td>400</td>
</tr>
<tr>
<td>10</td>
<td>Speleothem</td>
<td>Paraíso, Brazil</td>
<td>δ¹⁸O</td>
<td>Wang et al. 2017</td>
<td>4.07°S</td>
<td>55.45</td>
<td>60</td>
</tr>
<tr>
<td>11</td>
<td>Lake</td>
<td>Hill of Six Lakes, Brazil</td>
<td>pollen</td>
<td>Bush et al. 2004</td>
<td>0.30 °N</td>
<td>66.67</td>
<td>75</td>
</tr>
<tr>
<td>14</td>
<td>Lake</td>
<td>Carajás, Brazil</td>
<td>pollen</td>
<td>Absy 1991, Hermanowski 2012, Reis 2017</td>
<td>6.4°S</td>
<td>50.42</td>
<td>730</td>
</tr>
<tr>
<td>15</td>
<td>Marine</td>
<td>CDH-86, Brazil</td>
<td>XRF</td>
<td>Nace et al. 2014</td>
<td>0.33 °S</td>
<td>44.21</td>
<td>0</td>
</tr>
<tr>
<td>16</td>
<td>Marine</td>
<td>GeoB-16205, Brazil</td>
<td>pollen</td>
<td>Bouimetarhau et al. 2018</td>
<td>1.21°S</td>
<td>43.05</td>
<td>0</td>
</tr>
<tr>
<td>17</td>
<td>Marine</td>
<td>GeoB-3912, Brazil</td>
<td>XRF</td>
<td>Arz et al. 1998</td>
<td>3.67°S</td>
<td>37.43</td>
<td>0</td>
</tr>
<tr>
<td>18</td>
<td>Marine</td>
<td>GeoB-3910, Brazil</td>
<td>pollen</td>
<td>Behling et al. 2000</td>
<td>3.67°S</td>
<td>37.43</td>
<td>0</td>
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The graph illustrates the wet and dry cycles of the Western and Eastern Amazon regions over the past 20,000 years (Ka). The Western Amazon region alternates between wet and dry periods, with the dry phase occurring around 10,000 years ago. The Eastern Amazon region also experiences similar cycles, with a notable wet phase around the same time period. The graph spans from 0 to 20,000 years ago, with the y-axis representing wet and dry conditions.