Chapter 3
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 (Science 165: 131–137, 1969) Pleistocene refuge theory has provided motivation for 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 Pleistocene glacial-interglacial stages (~40 kyr and 100 kyr cyclicity), we highlight two aspects of Quaternary climate change in tropical South America: (1) an east-west precipitation dipole, induced by solar radiation changes associated with Earth's precessional variations

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(~20 kyr cyclicity); and (2) periods of anomalously high precipitation that persisted for centuries-to-millennia (return frequencies ~1500 years) congruent with cold "Heinrich events" and 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 became respectively 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 and speciation for others.

1 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 respectively 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 (Colinveaux et al. 1996; Bush et al. 2004). The contention was also 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; Prates et al. 2015). Yet phylogenetic studies across a wide range of plant and animal taxa increasingly point to the fact that many neotropical

Fig. 3.1 Biome map of tropical South America depicting the distribution of highland habitats (paramo and montane forests in the Andes and Guiana Shield region), rain forests (including Amazonia, Chocó, and the Brazilian Atlantic Forest), Patagonian steppes, grasslands (including the Cerrado, Chaco, Pampas, and Venezuelan Llanos), dry forests, xeric scrublands (including the Brazilian Caatinga), wetlands (including the Brazilian Pantanal), and Chilean Matorral scrublands

sister species did actually diverge in the Pleistocene (Richardson et al. 2001; Hughes and Eastwood 2006; Madriñán et al. 2013; Garzón-Orduña et al. 2014; Koenen et al. 2015; Byrne et al. 2016), opening the possibility of a role for Quaternary climate variation in the diversification of these biota (Rangel et al. 2018; Wheatley et al. 2019, but see Rull and Carnaval 2019 and Vargas and Dick 2019).

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. 3.1) and composition, to the limited extent that we know either. Finally, we briefly discuss the evidence from biogeographic and phylogenetic studies relevant to the question of how regional taxa may have evolved during, and in response to, periods of Quaternary climate change.

2 Climate Variability During the Quaternary

2.1 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 CO_2 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 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 kyr from 2.6 to ca. 0.8 Ma and higher-amplitude cycles every 100 kyr 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 low-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. 1999; 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. 2001a, b; 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. 3.2), from which we infer that western Amazon precipitation was high (i.e. comparable to modern) during the LGM (Table 3.1).
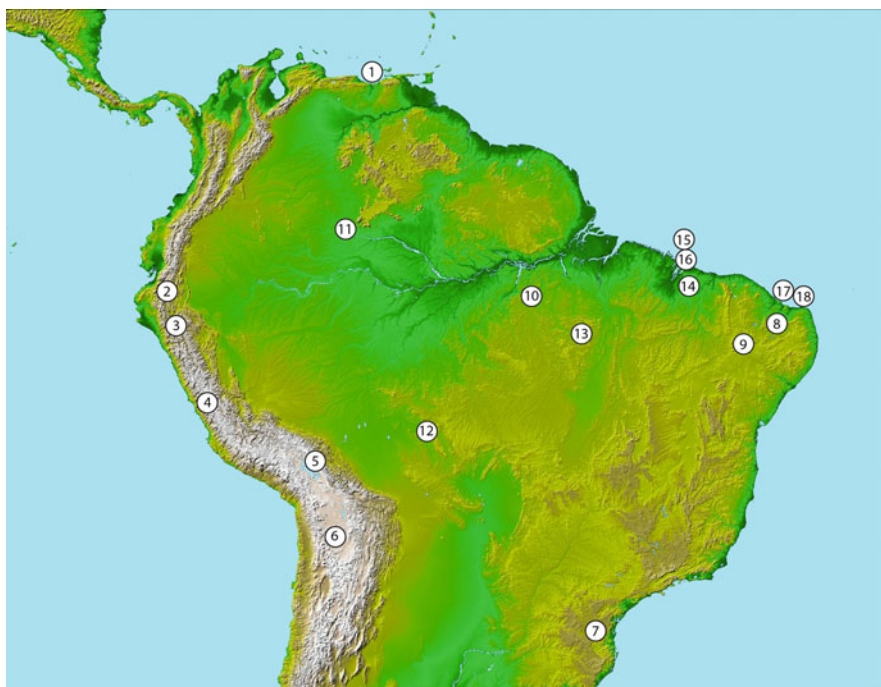
Fig. 3.2 Location of sites discussed in the text superimposed on a digital elevation model of South America. See Table 3.1 for site key and additional site details

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 et al. (2009) uncovered a precipitation dipole between the western Amazon/tropical central Andes and northeastern Brazil, varying with precessional (20 kyr) periodicity (Fig. 3.3). 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.

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 (Fig. 3.4) forced by

Table 3.1 Paleoclimate proxy records shown on the map in Fig. 3.2. The location and type of record, the measured proxy, and the authors responsible for each study are included

Site #	Archive	Record	Proxies	References	Lat.	Long °W	Elev. (m)
1	Marine	Caraico, Venezuela	Color	Peterson et al. (2000)	10.5°N	65	0
2	Speleothem	Santiago, Ecuador	δ^{18}O	Mosblech et al. (2012)	3.02°S	78.13	980
3	Speleothem	Diamante, Perú	δ^{18}O	Cheng et al. (2013)	5.73°S	77.5	960
	Speleothem	El Condor, Perú	δ^{18}O	Cheng et al. (2013)	5.93°S	77.3	860
4	Speleothem	Pacupahuain, Perú	δ^{18}O	Kanner et al. (2012)	11.24°S	75.82	3800
5	Lake	Titicaca, Bolivia/Perú	δ^{13}C	Baker et al. (2001a, b), Fritz et al. (2007, 2010)	16°S	68.5	3810
6	Lake	Uyuni, Bolivia	Gamma	Baker et al. (2001a, b)	20°S	68	3653
7	Speleothem	Botuverå, Brazil	δ^{18}O	Cruz et al. (2005)	27.22°S	49.15	230
8	Speleothem	Rio Grande, Brazil	δ^{18}O	Cruz et al. (2009)	5.6°S	37.73	100
9	Groundwater	Maranhao, Brazil	Noble gas	Stute et al. (1995)	7°S	41.5	400
10	Speleothem	Paraíso, Brazil	δ^{18}O	Wang et al. (2017)	4.07°S	55.45	60
11	Lake	Hill of Six Lakes, Brazil	Pollen	Bush et al. (2004)	0.30°N	66.67	75
12	Lake	Bella Viata, Bolivia	Pollen	Punyasena et al. (2008), Burbridge et al. (2004)	13.62°S	61.55	225
	Lake	Champlain, Bolivia	Pollen	Punyasena et al. (2008), Burbridge et al. (2004)	14.47°S	61.07	225
13	Lake	Carajas, Brazil	Pollen	Absy et al. (1991), Hermanowski et al. (2012), Reis et al. (2017)	6.4°S	50.42	730
14	Lake	Cacó, Brazil	Pollen	Ledru et al. (2006)	2.97°S	43.42	0
15	Marine	CDH-86, Brazil	XRF	Nace et al. (2014)	0.33°S	44.21	0
16	Marine	GeoB-16,205, Brazil	Pollen	Bouimetarhan et al. (2018)	1.21°S	43.05	0

Table 3.1 (continued)

Site #	Archive	Record	Proxies	References	Lat.	Long °W	Elev. (m)
17	Marine	GeoB-3912, Brazil	XRF	Arz et al. (1998)	3.67°S	37.43	0
	Marine	GeoB-3104, Brazil	Pollen	Behling et al. (2000)	3.67°S	37.43	0
18	Marine	GeoB-3910, Brazil	Pollen	Dupont et al. (2010)	4.25°S	36.34	0

Fig. 3.3 Sketch of the temporal evolution of precipitation of the eastern and western Amazon through one precession (20 kyr) cycle
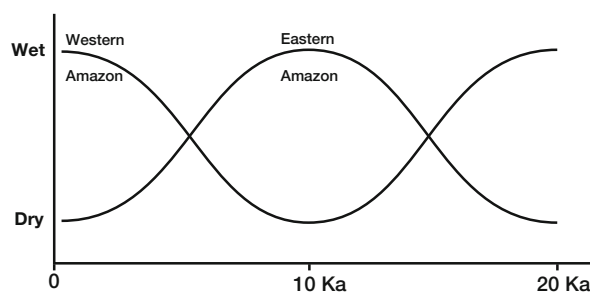
Fig. 3.4 A map of the east to west precipitation dipole in tropical South America on precession time scales (20 kyr) that shows the difference in DJF precipitation (mm d^{-1}) observed between low summer insolation (218 Ka) and high summer insolation (207 Ka) experiments. From Liu and Battisti (2015)
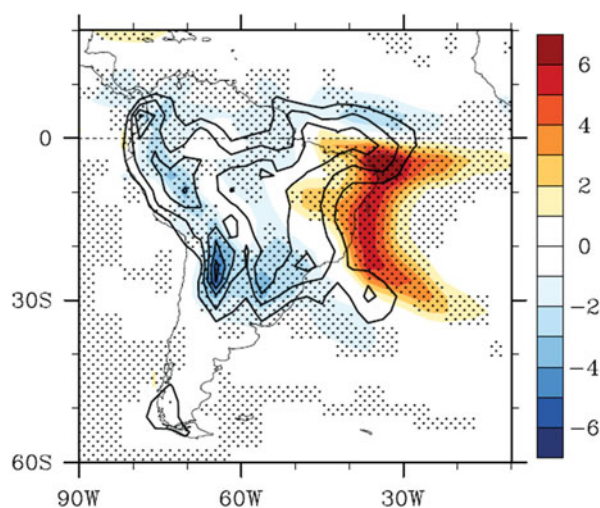
precessionally induced changes in insolation (Prado et al. 2013; Liu and Battisti 2015).

   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 Amazon 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 δ^{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. That is, LGM precipitation in the eastern Amazon was similar to modern precipitation in that region, although relatively low compared to contemporaneous precipitation levels from regions 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, 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 from the data that spatially variable regions of climate change and forest expansion/contraction (e.g. 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 divergence (see below).

2.2 Short-Term (Millennial) Extreme Precipitation Events: Were They Sufficient to Establish or Destroy Forested Habitat?

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 several hundred 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 90 and 10 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 is widespread

elsewhere in the Northern Hemisphere (Voelker 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. The regional instability associated with the occurrence of at least a couple dozen pulses of alternating increased and decreased precipitation over such a short period (i.e., ~80 ky) may have led to recurrent extirpation of forest organisms in northeastern Brazil. This dynamic may explain a pattern of lower species richness in eastern, as compared to the climatically more stable western, Amazonia (e.g., Jenkins et al. 2013).

Heinrich events are a second type of millennial climate variability during glacial stages, closely related to D-O stadials ("stadials" are the 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 far-field regions (Hemming 2004; Vellinga and Wood 2002). Paleoceanographic records from the Brazilian continental margin (Arz et al. 1998; Nace et al. 2014) document large increases of river runoff 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 $\delta^{18}O$ values (indicating peak wet conditions) in speleothem records from the central Andes of Peru (Kanner et al. 2012), the western Amazon (Mosblech et al. 2012; Cheng et al. 2013), and the eastern Amazon (Wang et al. 2017).

Thus, D-O stadials and Heinrich events had similar impacts on tropical South American climate (Fig. 3.5), 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 and extent. Ecological studies have found that the recovery of rain forest following disturbance happens quickly, within only a couple hundred years (Liebsch et al. 2008). Moreover, vertebrate species can diffuse through thousands of kilometers of suitable
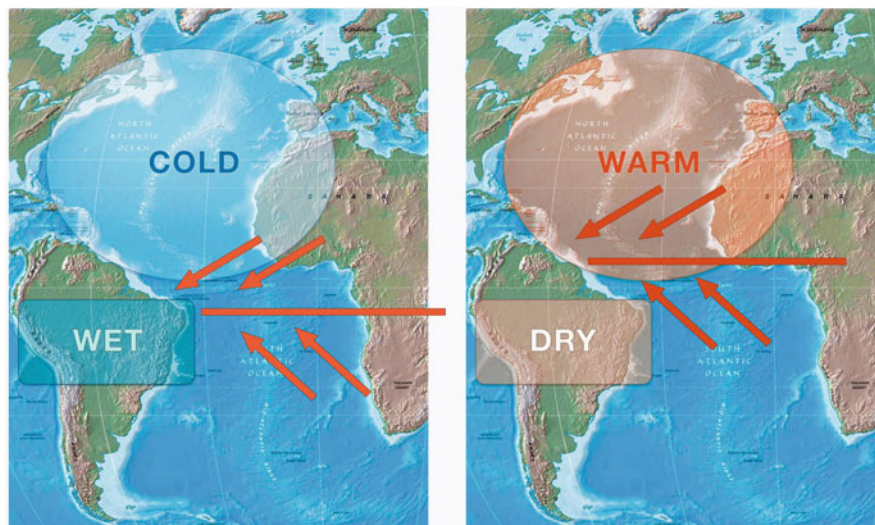
Fig. 3.5 A sketch of the impact of millennial cold and warm variability in the North Atlantic region on the position of the ITCZ and trade winds and on precipitation throughout tropical South America. See text for additional details

habitat within only a few decades, as suggested by ecological studies of amphibian, mammal, and bird species (Phillips et al. 2007; Stodart and Parer 1988; Wehtje 2003). As a result, the temporal scale of the climatic shifts implicated in D-O stadials and Heinrich events certainly was sufficient to lead to pronounced changes in habitat and species distributions in northern South America.

3 Biological Responses to Quaternary Climate Variation

3.1 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 western to central Amazon (e.g., Cheng et al. 2013) has major implications for evolutionary studies of other organisms associated with forest settings. For instance, some animal populations may have remained stable even when faced with temporal turnover of

tree species, as long as the structural forest environment remained similar over time. Yet, the paucity of sites in 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 variability in the distribution and species composition of regional biomes through time (Fig. 3.1). While the available information points to stability of wet tropical forests in western to central Amazonia, 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). However, phylogenetic evidence of dispersal events through gallery forests in the open habitats of central and northern Brazil is currently lacking.

Phylogenetic patterns in distinct organisms suggest links between Quaternary climate variation and population divergence. Patterns of genetic structure in species that colonized the Atlantic Forest from Amazonia indicate population genetic differentiation following forest contraction and biome separation (Dal-Vechio et al. 2018; Prates et al. 2018). These climate-driven events of population divergence, inferred to have happened recently, provide a mechanism to explain speciation and new evolutionary radiations also at deeper timescales. 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.

Lastly, climatic stability may contribute to the accumulation of biodiversity at regional spatial scales. In an example from the Atlantic Forest region, Carnaval et al. (2009, 2014) tested whether vertebrate phylogenetic endemism was related to forest persistence over the last 120 kyr. Their analysis, using climate model output, suggests that forest stability was a necessary factor for maintaining high levels of lineage endemism. However, different factors best explain patterns of endemism in the northern and southern regions of the Atlantic Forest; whereas lineage endemism is better predicted by climatic stability through time in the north, spatial climatic heterogeneity was a more important predictor of lineage endemism in the south. Such examples of integration of geologic and genetic approaches (geogenomics, *sensu* Baker et al. 2014) provide a potentially powerful means of testing models of how climatic history has affected evolutionary history and shaped current spatial patterns of biodiversity.

3.2   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 tree taxa (e.g. *Podocarpus*) descended to the lowlands and expanded through the Amazon forest in response to past climate cooling (Colinveaux et al. 1996), creating assemblages that have no modern analog (Bush et al. 2004; Reis et al. 2017). These episodes of range expansion, 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 vertebrate taxa point to the establishment of rainforest corridors connecting eastern Amazonia with the northern Atlantic Forest in northeastern Brazil during the Pleistocene (Batalha-Filho et al. 2013; Dal-Vechio et al. 2018; Prates et al. 2016a, b, 2018). 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 dispersal.

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

An increasing number of studies support a direct link between Pleistocene climatic variability, dispersal, and speciation in tropical South America. Several groups of lowland rain forest and Andean taxa diversified 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), and patterns of phylogenetic structure in birds, mammals, and reptiles support pulses of forest expansion that are spatially congruent across taxa, such as in present-day northeastern Brazil (Batalha-Filho et al. 2013; Costa 2003; Dal-Vechio et al. 2018; Prates et al. 2016b). The timing of population divergence and speciation for many taxa, as well as the inferred routes of range shifts, match expectations derived from the known variability of Pleistocene climate. These large-amplitude climate shifts extended not only into the Amazon basin but also into higher elevations in the tropical Andes.

Pleistocene climate variability superimposed upon pre-existing Andean topography provides a mechanism for driving speciation in high relief terrains. It has been suggested for plants (Gentry 1982) and frogs (Santos et al. 2009) and recently modeled (Rangel et al. 2018; Wheatley et al. 2019) that a significant proportion 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), many Andean diversification events are recent, overlapping with the timing of Quaternary climatic dynamism (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 taxon-specific effective porosity is related to their width, depth, and the physiological tolerances of different organisms (e.g., Wiens 2004). 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 2019).

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 climate-driven dispersal followed by isolation on mountain tops, a mechanism similar to that proposed for the Andes. Moreover, novel taxa originating in these high elevation habitats adjacent to Amazonia may have dispersed downward, providing lineages to central Amazonia (Santos et al. 2009).

Another important layer needed to improve our understanding of how Quaternary climate change affected neotropical biotas is the synergistic 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.

Climate variability may also help to explain attributes of ecological communities. This is the case, for instance, in the observation that many tree species in the Amazon region are rare. It is possible that the low abundances of these species represent population declines in response to climatic shifts, while more favorable climates in the past may have sustained larger populations. Similarly, periodic mixing and population changes associated with spatio-temporal climate variability may explain why Amazon tree communities are widely dispersed and appear to have little community phylogenetic structure (Dexter et al. 2017). Lastly, climate variability may also help to explain how drought-tolerant and drought-intolerant plant species come to reside in the same forests (Esquivel-Muelbert et al. 2019).

4 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. For instance, the western Amazon, the central Andes, and the southeastern sub-tropics were similarly wet as at present during the LGM, 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 brought about pulses of forest expansion and contraction. Biogeographic investigations of forest taxa recovered population changes and speciation events within the temporal and spatial scales implicated in climatic change associated with the precession cycles, Heinrich events, and D-O stadials. These pulses of climate-driven habitat shifts had dramatic effects on the composition of regional species pools and likely contributed to diversification. For instance, changes in habitat distribution led to connections and biogeographic exchange among presently distinct neotropical biomes, such as Amazonia

and the Atlantic Forest. Moreover, forest contraction concomitant with the expansion of open and dry regions (such as the Cerrado and Caatinga) led to separation of major forested regions; isolated in these "mega-refugia", forest populations diverged and became new species, and species became new clades. The genetic evidence also supports that Quaternary climate variation promoted explosive radiations in the regions of high topographic relief surrounding central Amazonia, which subsequently provided lineages and increased the diversity of lowland forests. New biological and paleoenvironmental data convincingly support that Quaternary climate variation played a major role in evolutionary diversification in tropical South America. The responses of co-distributed organisms to these climate dynamics may have been mediated, to some extent, by distinct ecological tolerances and their underlying physiological and life history traits (Prates et al. 2016a, b).

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