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Climate changes and speciation pulses in a nearly flooded continent: tackling the riddle of South America's high diversity

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ABSTRACT

Understanding the origin of South America's diversity is of great importance especially considering our current extinction crisis in the face of climate change. While great debate exists about the sources of Amazonian diversity, there is no consensus about an overarching process that explains the Amazon's uniquely high diversity. In this contribution, I present the following model considering the impact of tectonics on the hydrology of the continent. When the Andes rose, it dammed the paleo-Amazon, which ran west at the time. This produced generalized flooding with a mosaic of forest in the more elevated areas surrounded by flooded habitats. Because of the flat relief of the Amazon basin, small changes in water level produced forest expansion and contraction, resulting in speciation pulses. Using data from the literature on species distribution, as well as the age of new lineages from molecular studies, I show that the space and timing of speciation process in the South America was consistent with the predictions of this model. This model also posits that there were no marine incursions on the continent. Rather, marine conditions developed *in situ*, might be a better explanation for the marine conditions found in paleo-history of the region. This model provides a theoretical framework for evolutionary processes in South America that explains its uniquely high diversity.

KEYWORDS
Amazon, biodiversity, macroevolution, paleo-ecology, speciation.

INTRODUCTION

As the World heads deeper into the most recent extinction crisis, in the face of climate change, understanding the sources of biodiversity becomes all the more important. The global trend of higher species in lower latitudes has been well established for many years (Humboldt, 1850; Pianka, 1977; Antonelli *et al.*, 2018). A lot of the debate has focused on whether tropical areas are cradles of diversity that have more species because they have higher speciation rate; or museums, that have

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higher diversity because they have a lower extinction rates, or a combination of both (Fjeldså, 1994; Voelker *et al.*, 2013; Weir, 2006). Within the tropics the Amazon basin stands out as the most diverse terrestrial ecosystem in the world; with greater diversity of organisms across taxa than any other tropical region (Haffer, 2008; Rull, 2011, 2015). The causes of this biodiversity have been the matter of persisting debate, but to the present there is no consensus on its origin.

For years the *Refugia Hypothesis* was viewed as the sole explanation for tropical high diversity. It postulates that during Pleistocene glaciations rainforest contracted to isolated patches surrounded by savannah (Haffer, 1969; Prance, 1982). When warmer periods returned, the forest expanded again, reconnecting all the refuges. Populations separated during the forest contraction events had accumulated enough mutations that they were no longer able to interbreed, resulting in new species. These vicariant events associated with the contraction and expansion of the forest produced speciation pulses that resulted in high diversity (Duellman, 1982; Haffer, 1982). However, the *Refugia Hypothesis* has been discredited lately. Recent pollen studies show the permanence of pollen transported by insects or other animals, not wind, and suggesting that the whole area has been covered by forest since the Miocene (Bush & Oliveira, 2006; Colinvaux & De Oliveira, 2001; Colinvaux *et al.*, 2000). Furthermore, molecular studies show that a lot of the speciation processes that are responsible for the high diversity occurred during the Miocene before the Pleistocene glaciations took place (Moritz *et al.*, 2000; Rull, 2008, 2011), and, recent evidence based on the distribution of forest specialists shows that forest patches expanded, not contracted, during the Last Glacial Maximum (Leite *et al.*, 2016). Combined, these lines of evidence debunked the *Refugia Hypothesis*.

Current notions about speciation processes in the Amazon are mostly taxa specific and invoke several processes (Haffer, 2008) such as neutrality (De Aguiar *et al.*, 2009; Hubbell, 2001; Latimer *et al.*, 2001), predation (Leigh Jr *et al.*, 2004), heterogeneity of sediments (Fine *et al.*, 2005), and the river effect (Hayes & Sewlal, 2004). The River effect has been advocated as a strong source of diversity by creating and separating land masses which allow allopatric speciation between different habitats (Haffer, 1992). Data shows that the river effect helps to create and maintain diversity in some areas but the evidence is ambiguous in others (Jackson & Austin, 2010; Voelker *et al.*, 2013; Naka & Brumfield, 2018). Changes of riverbeds during recent times might confound phylogenetic trends and the barriers that caused them, as some diversity trends might be responses to previous barriers. In the Guyana shield where rivers are hard set, the river hypothesis holds better than in the Amazon Basin where the riverbeds are loosely defined (Naka & Brumfield, 2018) (Table 1).

While the processes described above are likely important in regional specific speciation processes, there is no consensus about an overarching process as the main driver for the Amazon's high diversity (Bush, 1994; Haffer & Prance, 2001; Haffer, 2008; Hayes & Sewlal, 2004; Rull, 2011, 2015). More importantly, there is still a big piece of the puzzle missing. All these processes apply equally for all tropical regions. Yet, South America stands alone in terms of their species diversity compared to other tropical landmasses. A recent study on bird diversification (Claramunt & Cracraft, 2015) provides data on lineages and endemic species present in different biogeographic regions. Figure 1, made with data from the supplemental material of this study, shows how most tropical biomes have a comparable number of lineages (families), but when it comes to endemic taxa, South America is in a league of its own. The higher number of endemic families and endemic species found in South America suggests that South America have had higher levels of speciation for a relatively long time. We would find a similar picture if we were dealing with other taxa such as freshwater fishes (Albert *et al.*, 2011), amphibians (Santos *et al.*, 2009; IUCN, 2017), bats (Lim, 2007; Teeling *et al.*, 2005) (Armstrong *et al.*, 2014). Thus, an explanation for the high diversity of South America that is unique for the continent is still lacking. In the following section I propose a hypothetical model aimed to explain South America's unique high diversity by taking into consideration the effect of tectonics and hydrography in the biogeography of the continent, which has been largely ignored.

The Big Dam (and Big Swamp) Hypothesis.- When South America separated from Gondwana (approx. 120–112 Mya), it was mostly drained by a large river very much where the Amazon River is currently located, but it ran west into the Pacific Ocean, the paleo-Amazon. As South America collided with the Nazca plate, subduction of the latter initiated the rise

TABLE 1 Summary of different hypothesis explaining the tropics high diversity.

Hypothesis	**Rationale**	**Unique to South America?**	**Reference**
Refugia	Forest expanded and contracted during the Pleistocene in response to climate fluctuations producing speciation pulses	No	Haffer (1969)
River	Rivers act as vicariant barrier producing allopatric and peripatric speciation	No	Hayes & Sewlal (2004); Ribas *et al.* (2012); Crouch *et al.* (2019)
Predation	Predators produce Paine effect preventing prey species to outcompete other, thus keeping high diversity	No	Terborgh (1992); Leigh Jr *et al.* (2004)
Neutrality	All individuals are equivalent to each other so species are not competing or excluding each other	No	Hubbell (2001); Latimer *et al.* (2001); De Aguiar *et al.* (2009)
Interspecific competition	Competition leads to specialization over evolutionary time which allows for higher species packing	No	Terborgh & Weske (1975); Terborgh *et al.* (1990)
Intermediate disturbance	Regular intermediate disturbances reset competition among species preventing one from excluding the others	No	Molino & Sabatier (2001); Roxburgh *et al.* (2004); Crouch *et al.* (2019)
Productivity	More resources allows for more individuals which increase the changes of more species	No	Schoener (1971); Janzen (1976); Sayer *et al.* (2010)
Big Dam	The raise of the Andes damned the paleo-Amazon flooding the continent. Small climate fluctuations produced contraction and expansion of habitats leading to multitude of vicariant events going back until the early Miocene other	Yes	This contribution

of the Andes, blocking the westward flow of the Paleo-Amazon and closing off its connection with the Pacific Ocean (Latrubesse *et al.*, 2010; Lundberg *et al.*, 1998). Continued subsidence of the Nazca plate produced ridges of flexural forebulges, extending east from the Andes that would have resulted in higher ridges separated by lower depressions between them (Bicudo *et al.*, 2019). The original paleo-Amazon drained most of the area currently drained by the Amazon and Orinoco Rivers. Since this was a very warm period, it is expected that the continent was at least as moist as it is now; so, this river must have been a true colossus. It follows that raising a 7,000 km long dam to this river would result in a nearly total continental flooding. Up to the present models about South America paleo-ecology seem to ignore the likely flooding that this spectacular volume of water would have done on the continent. The foundations of the Big Dam Hypothesis (hereafter BDH) consider existing models but include the effect that the water of the dammed river would have had on vicariant events both

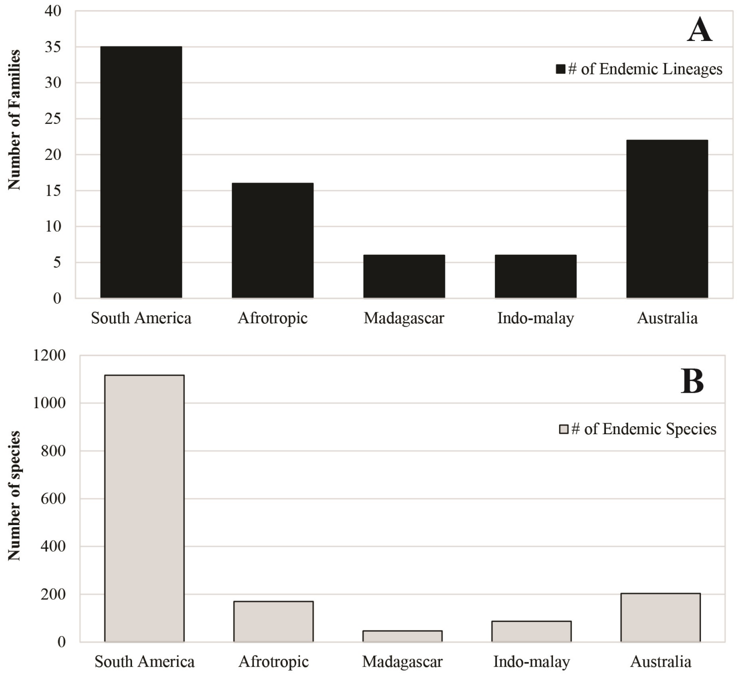

FIGURE 1 **(A)** Number of endemic linages (families/subfamilies) present in the Tropical biomes across the world. **(B)** Number of endemic species present in different tropical regions. Data were obtained from Claramunt & Cracraft (2015) supplemental information by extracting those lineages that only occur in one of these biogeographic areas. The number of endemic taxa is a consequence of the intrinsic diversification rate of each biogeographic unit. South America number of endemic species is one order of magnitude higher than their paleo-tropical counter parts. The fact that the number of endemic lineages is also higher than the others suggests that the high diversification rate of South America have been in place for a relatively long time. The data for this figure is provided in the supplementary material.

in land and water.

The damming of the paleo-Amazon, that is estimated to have started some 90 million years ago, would have been a very gradual process (Hoorn *et al.*, 1995; Lundberg *et al.*, 1998; Latrubesse *et al.*, 2010). It would have begun with the mouth becoming progressively shallower, which would have resulted in the river backing up and flooding its flood plains initially. As the Andes continued to rise, it would have increasingly limited the drainage of the river, and its waters would have flooded most of the lowlands of the western part of the continent until the water level was high enough to spill into the ocean in whichever direction was lower. Data shows that at least part of it spilled to the north via the Llanos/Magdalena basin and drained into the Caribbean via what is currently northern Venezuela and northeastern Colombia. Some of it may have also drained over the lowlands between the Southern Andes and the Brazilian Shield via the Madre de Dios and current Pantanal (Mora *et al.*, 2010; Wesselingh & Hoorn, 2011).

The flow of this river was perhaps similar to the current Pilcomayo in Bañado La Estrella, northern Argentina; where the river runs slowly in a very broad, shallow path without a clear channel (Díaz de Gamero, 1996). This big river, that has been called paleo-Amazonas-Orinoco system (Lundberg *et al.*, 1998) for its northern direction, would have produced abundant marshes on its sides, scattering the landscape with lacustrine systems surrounded by different kinds of rainforest depending on its elevation. Higher elevations, as in the ridges of the flexural beluges, piedmonts, and river banks, would have had Terra Firme forest and other areas with lower elevations would have had flooded forest of lower canopy height such as Várzea or Igapós, even if the floristic compositions of these types of forest had been quite different from their contemporary equivalents (Pires & Prance, 1985; Daly & Mitchell, 2000; Cordeiro-Bicudo *et al.*, 2019). These are different kinds of "rainforest" with differences in level of flooding, water quality, canopy height, and understory composition. Areas that received nutrient rich water from the Andes became "white water" systems including Várzea forest; while waters from the deeply weathered and highly leached soils of the Guyana and Brazilian shields would have been far more oligotrophic (Vonhof *et al.*, 2003; Wesselingh & Hoorn, 2011). These waters would have produced "clear water" bodies if they were running, but in lacustrine systems or in flooded Igapó forest, the decomposition of leaves released tannins that turned them into acidic "black water" systems (Prance, 1979; Daly & Mitchell, 2000). Blocking the big river would have also produced other areas of permanently flooded marshes or swamps where tree growth was impeded due to the flooding regime (Prance, 1979). In fact, there are evidence of swamps, grasses, and extensive treeless areas in the amazon paleo-history (Latrubesse *et al.*, 2010; Hoorn *et al.*, 2017). Perhaps this system was similar to what we find currently in the Llanos or Pantanal (Mittermeier *et al.*, 2002; Rivas *et al.*, 2002) but in a much large spatial scale.

In the extremely flat relief of the basin (ca. $8.3 \text{ x}10^{-3}$ percent), a small vertical difference in the water level represents a very large horizontal difference in the flooding area. So, a relatively small increase in precipitation would produce substantial vicariant events connecting flooded habitats and isolating Terra Firme. An equivalent drop in precipitation would reconnect Terra firme, and isolated aquatic habitats, producing speciation pulses in both systems. These would have been pulses of flooding equivalent to the current yearly flooding pulses of the Amazon (Erwin & Adis, 1982) but these would have been in a larger temporal and spatial scale. Due to their larger spatial scale it would have resulted in genetic separation of populations; and because of its larger temporal scale, it would have resulted in enough time for populations to start speciation process. Basically, the BDH flips the *Refugia Hypothesis* on its head. The refuges were not ecological islands of forest surrounded by savannah, but islands of Terra firme surrounded by a mosaic of other more flooded habitats.

The conditions described above likely remained for several million years. There may have been at least semi-flooded conditions dating back to the Late Cretaceous as the outlet of the Paleo-Amazon became shallower and could not drain all its water. Approximately 24 Mya, the continuous uplifting of the Andes created a mega-wetland that developed in Western Amazonas, the Pebas system. This mega wetland is believed to have been flooded because of cratonic deformation. As the Andes rose the Cratonic Basin deformed producing elevations below sea level to the east that would have allowed water from the Caribe to progress into the continent (Hoorn *et al.*, 2010b). However, just at the beginning of the Pebas system is the time when the connection with of the great river and the Pacific Ocean would have been severed. So, the flooding of the Pebas system can also be explained with the water from the mighty river. This explanation is more parsimonious than the ocean transgression because (1) it does not require such a drastic bending of the South American Craton to allow the ocean to invade thousands of kilometers into the continent; (2) the current explanation assumes that the continent was dry (not flooded). Otherwise the ocean could not have made any progress into the continent because of the dammed river would have prevented the ocean to come even if the craton was deformed below sea level. Likely, it would have resulted in some salinity in the mouth of the estuary such as they are found currently in Maracaibo Lake in Norther eastern Venezuela, but not marine conditions (Vonhof *et al.*, 2003). So the notion that the ocean came into a dry continent because of cratonic deformation assumes the, unlikely, disappearance of a spectacularly large volume of water. In fact, studies from isotopes from mollusk shells shows that the water of this system was essentially fresh water (Vonhof *et al.*, 2003).

Flooding regime in the area would have become more intense as the Andes reached higher elevation. All this time South America continued receiving moisture through Atlantic trade-winds but the air masses that left the continent, after raising pass the Andes, were dry. This resulted in South America sequestering large amounts of global moisture (Mörner *et al.*, 2016). As the Andes rose, the amount of sediments in the Pebas system increased, filling it up. The mostly-flooded wetlands would have slowly transitioned toward a less-flooded ecosystem as sediments from the Andes filled up the Pebas system, creating the Acre system 10 Mya. This eventually filled up too; leading to the current drainage direction of the Amazon, which began around 7 Mya (Hoorn *et al.*, 2010a). Even after the Amazon started flowing east, there likely remained many extensions of virtually 0 slope that still produced forest contraction and expansion with small differences in precipitation or regional climatic fluctuations (Strecker *et al.*, 2007; Mora *et al.*, 2010; Vonhof & Kaandorp, 2010). So, this system of a semi-flooded continent would have experienced forest contraction and expansion with relatively small fluctuation in precipitation, starting probably early in the Cenozoic and lasting until relatively recently.

Unlike the *Refugia Hypothesis*, the described model here does not require a full-blown glaciation to produce speciation pulses. Rather, much smaller changes like, say, Milankovitch cycles, would have sufficed. In fact, local and regional changes in precipitation on the continent could result in local expansion and contraction of forest without the need of a world-wide climate change (Sepulchre *et al.*, 2010). There is no need of an arid ecosystem or savannah-like habitat to develop to produce vicariant events, so it is compatible with the paleolimnological evidence of presence of forest throughout the continent. Because the initial damming of the river may have started as early as the Late Cretaceous, the BDH can explain diversification processes that occurred much farther back than the Pleistocene. It is also explains why Terra Firme actually expanded during glacial/dry periods (Leite *et al.*, 2016).

Furthermore, species pulses were not limited to dry land. Movement of aquatic animals among these flooded systems was probably prevented due to the large difference in water quality between the different flooded habitats (Ferreira *et al.*, 2010). Even small variations in precipitation patterns within the basin would have produced a predominance of white water systems at times when the Andes provided most of the water (Sepulchre *et al.*, 2010). At other times, the older formations could have provided black water pulses, disrupting and fragmenting white water ecosystems and producing species pulses among aquatic organisms.

There have been several reports of marine transgressions from the Caribbean into the western Amazon, yet there is considerable debate in how and where these marine incursions took place (Díaz de Gamero, 1996; Wesselingh & Salo, 2006; Hovikoski *et al.*, 2010; Jaramillo *et al.*, 2017). It has been assumed that the path was via northwestern Venezuela in what is currently Zulia and Falcon states. However, Díaz de Gamero (1996), conclusively debunks this hypothesis based on the nature of the sediments and the volume of the ancient river. The BDH posits that these ocean transgressions never occurred. A very large river draining into the Caribbean would have prevented seawater from getting into the continent at all (Díaz de Gamero, 1996). Whatever world-wide meteorological conditions increased sea levels substantially would have also increased proportionally the amount of water on the continent making the volume of the paleo-Amazon-Orinoco all the larger. Whether for ocean level's rise, or for cratonic deformation, the river's fresh water would have accumulated, matching the sea level and keeping the ocean at bay. This is not that different than what happens today in the deltas of big rivers, such as the Orinoco or Amazon, with the tide cycle (Archer, 2005). When the ocean tide rises, it dams the river and makes it go up, but the marine water does not make any substantial progress into the continent.

Although marine incursions are a big part of South America Paleogeography, there has never been any evidence of such marine incursions. Rather, marine incursions have been assumed due to the presence of marine conditions such as the presence of foraminifera and mollusk shells, pollen from mangroves, and a variety of fishes from marine or estuarine lineages (Hoorn, 2006; Roddaz *et al.*, 2006; Wesselingh & Salo, 2006; Wesselingh *et al.*, 2006; Boonstra *et al.*, 2015). Yet, these are only evidence of "marine conditions"; these marine conditions could have developed *in situ*.

Clearly the only way to explain marine conditions in a dry continent is by assuming an unlikely marine transgression of thousands of kilometers into the continent. However, if the continent was flooded marine conditions can appear very readily. Dry periods or regional weather fluctuations could result in freshwater bodies turning haline. They did not have to be dry enough to produce arid vegetation on the continent, just dry enough that the big river had such low water that the wetlands became fragmented and some parts of the estuary stopped flowing, and voiding sediments into the Caribbean (Vonhof *et al.*, 2003). The fluvial system would transition, at least in some places, to lacustrine at first, and eventually its water would have become haline enough to allow the development of marine organisms from estuarine stocks. It would have been some sort of mosaic of conditions where larger water bodies, or those with good input of water from higher elevations, remained relatively fresh, but shallower extensions of the estuary, or lower elevation that did not drain into the other water bodies, would have developed fully marine conditions. There would have also been all the intermediate stages scattered across the landscape. Areas that received waters from the nutrient rich Andes would have become haline faster than those receiving water from the oligotrophic Guyana and Brazilian shields. In fact, establishment of haline conditions of estuaries during dry periods occurs today in tropical estuaries (Valle-Levinson & Bosley, 2003; Carrillo *et al.*, 2009), except that this was a much larger spatial and temporal scale.

In this contribution, I make predictions based on the BDH as a framework for the evolution of South American diversity and test them using information from the literature on the geological events of the continent and the appearance of new species in different crown lineages in space and time. I revise the evidence for marine incursions and provide explanations based on the BDH that explain the data as well, or better, than the existing explanations. The BDH does not attempt to replace other hypothesis that explain high diversity, but rather to provide a historical framework where the different hypotheses work in synergy to explain the high diversity. While the evidence presented here is largely correlational, the goal of this study is to contribute with a new paleo-ecological scenario that has not yet being considered and that has the potential to explain a lot of the questions that remain unanswered.

METHODS

***Testing the Big Dam Hypothesis*.-** The BDH posits that South America was subjected to variable levels of flooding throughout the Cenozoic. Changes in flooding regime would have resulted in expansion and contraction of both forest islands and aquatic ecosystems resulting in vicariant events under both conditions. Based on this scenario, I make the following testable predictions: (1) endemism centers of terrestrial taxa would be found at higher elevations; (2) speciation processes across taxa did not occur at random through the history of South America. Rather, several clades would have speciation bouts at the same time while there would be periods were no, or few, new lineages emerged. Because the BDH suggests that the flooding of the continent would have prevented marine incursions and that the Marine Derived Lineages (MDLs) found in South America descend from estuarine stock that were trapped following disconnection from the ocean, (3) no strictly marine or steno-haline fossils should occur in South America. In the following sections I attempt to provide evidence supporting the BDH model and the posed predictions using data from the literature.

***Speciation in Space*.-** Using the current distribution of birds (mostly Terra Firme specialists) and current precipitation patterns, Haffer (1969) speculated about the location of the Pleistocene forest refuges that kept forest while the rest of the continent became semiarid. However, we now know that South America did not undergo the dry periods that the *Refugia Hypothesis* required (Bush & Oliveira, 2006; Colinvaux & De Oliveira, 2001). Under the BDH, refuges were Terra Firme islands that did not flood in periods when the water level rose. So, the BDH predicts that these refuges identified by Haffer were associated with higher elevations compared to their surroundings.

***Speciation in Time*.-** To assess the origin of species over time, I used the divergence dates of new lineages from existing molecular phylogenies. Since I only consider extant lineages this analysis does not take into consideration changes in extinction rates. Rather it focuses on times when the number of extant lineages increased vs times when it did not (Morlon, 2014). The number of lineages could increase because there were bursts of new lineages with constant extinction rates, because there were bursts of extinctions with constant speciation rates, or a combination of both. Since these are relatively new lineages and that the continent has not experienced catastrophic events in the period of study, I will assume that the increase of new linages is the consequence of increased speciation rates under a constant background of extinction rates.

The BDH predicts that speciation rates increased when the Andes became a tall mountain range and trapped a lot of the continental moisture producing speciation pulses with small climate changes. It also posits that the speciation processes occurred in cycles across the continent producing vicariant events that would have affected a variety of taxa. So, new lineages would appear in synchrony in different groups. Rull (2008) gathered samples of crown lineages that were unbiased both taxonomically as well as geographically within South America. I graphed the cumulative number of lineages present over the last 26 My looking for periods where there were increases in the number of lineages and others where no new lineages appeared. Furthermore, I used Rull's dataset to calculate the expected number of new lineages appearing every 500 Ky. I divided the number of new lineages in every time period by the number of exiting linages at the time. This gave me an average rate of lineages production per 500 Ky over the last 26 My. I used this fraction to calculate the expected number of new species per time period under the assumption that new lineages appear at random, depending only on the number of existing lineages. I multiplied the average rate of appearance of new lineages found in the continent, by the number of lineages present, and compared it with the actual number of new lineages of that time period using a Kolmogorov-Smirnov test. The BDH predicts that the number of new species in every interval will be different than that predicted by the number of existing lineages, sometimes higher sometimes lower.

To further test how the conditions under the BDH model might have affected the appearance of new lineages, I used molecular studies from a variety of taxa to explore the synchronicity of speciation events among Sigmodontine mice (Parada *et al.*, 2013), army ants (Brady, 2003), ovenbirds (Furnariidae) (Irestedt *et al.*, 2009), Attini ants (Ward *et al.*, 2015), primates (Perelman *et al.*, 2011), Conopophagidae passerines (Batalha-Filho *et al.*, 2014), basal snakes (Colston *et al.*, 2013), armored catfish (Loricaridae)(Silva *et al.*, 2016), and piranhas (Serrasalmidae) (Thompson *et al.*, 2014). Also, to test the effect of the influence of the Andes height on speciation rates, I calculated a partial correlation between the ages of new lineages over time and the elevation of the Andes at that time (Garzione *et al.*, 2008). If the elevation of the Andes had an independent effect on speciation, the BDH would predict an increase in the appearance of new lineages, as the Andes became a taller mountain range. Because more lineages will likely produce more species I used a partial correlation to remove the effect of number of lineages present. Also, to test the synchronicity of the appearance of new lineages I calculated a Spearman rank correlation with the time of appearance of new lineages across these taxa. A high correlation value would result if several taxa producing new species, or not, in synchrony. Statistical analysis were done with SPSS (IBM Corp., 2011). The data used in all these calculations are included as supplementary material.

***Marine Incursions* vs. *in situ Marine Conditions*.-** The BDH posits marine incursions in the continent were unlikely. Rather, marine conditions developed *in situ* in some of the internal lakes and swamps of the Big Dam associated with dry spells or other changes in meteorological conditions. Internal marine conditions would have developed during drier periods associated with eustatic drops in sea level when the Big Swamp stopped voiding sediments into the ocean. This could have occurred associated with cooling periods when the planet's water was sequestered in glaciers. Alternatively, regional climate conditions could have produced localized droughts in South America independent of major world-wide conditions, or otherwise provided conditions for haline environments to develop in internal waters. True ocean incursions are supposed to be worldwide events associated with warmer periods when the icecaps melted providing the water for worldwide rising of the oceans. I looked at global reconstruction of the world's paleo-climate (Zachos *et al.*, 2001, 2008) and eustatic sea levels (Hansen *et al.*, 2013) seeking correlation between temperature fluctuations, sea levels, and marine conditions on the continent. The prediction during a true marine incursion is that the temperatures will be higher with higher sea levels worldwide. The prediction of marine conditions developed *in situ* is that they were associated with cooling periods or periods of lower sea level.

RESULTS

Recent studies on South America biodiversity sustain that the distribution of variety of taxa, is strong indication of the origin (Honorio Coronado *et al.*, 2015; Guedes *et al.*, 2018; Crouch *et al.*, 2019). The avian refugia identified by Haffer (1969) were in fact places of higher elevation. The Figure 2 shows these refuges on an elevation map, and it is apparent that they would have maintained Terra firme forest in times of flooding. Simulation of different elevations of South America over the last few million years also supports the notion that Haffer's refuges were, in fact, higher elevation areas (Cordeiro-Bicudo *et al.*, 2019).

The record of new crown lineages appearing on the continent from Rull (2008) is presented in Figure 3A. It is possible to see a ladder-like pattern with periods in which the number

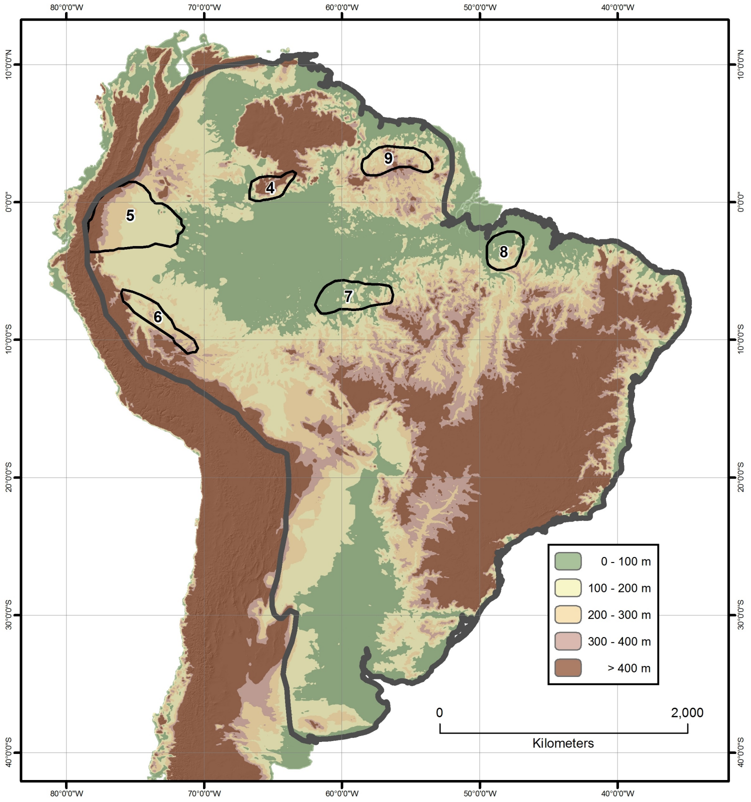

FIGURE 2 Elevation of Haffer (1969) proposed bird Pleistocene refuges on an elevation map. Numbers correspond to Haffer's original numbering of Pleistocene refuges: Imerí Refuge (4), Napo Refuge (5), East Peruvian Refuge (6), Madeira-Tapajós Refuge (7), Belen Refuge (8), and Guaianan Refuge (9). Map by J. Zebrowski.

of lineages did not change and brief periods when there was a jump in the number of lineages over time. This discontinuity of the cumulative number of lineages suggests that new lineages appeared in pulses throughout the Miocene. This figure also shows a sharp increase in the last 6 My coincident with the last uplift of the Andes (Gregory-Wodzicki, 2000), when a radical change in the drainage of the continent took place (Hoorn *et al.*, 2010a). Using the same dataset, Figure 3B shows a histogram with new lineages appearing and the predicted number of lineages expected based on the number of existing lineages. It is clear that there are burst of new lineages alternated by pauses in the appearance of new lineages, which significantly differs from what would be expected by chance (Kolmogorov-Smirnov, Z = 2.25, $P < 0.001$).

After removing the effect of the cumulative number of species with a partial correlation test, the appearance of new species is positively correlated with the height of the Andes more than expected by chance ($\beta = 0.24$, $n = 66$, $P = 0.05$, 2-tailed test), suggesting an independent effect of the Andes' height on speciation processes. A Spearman Rank correlation suggests synchrony in the appearance of species across a variety of taxa from the literature (Table 2). A positive correlation between two lineages means that those lineages had pulses with new species and pauses of speciation at the same time, supporting the BDH. This pattern seems clearer among ectotherm vertebrates and fishes, but not so much among ants and basal snakes. Figure 4 shows the appearance of new species among those endotherms with high mobility (birds and monkeys). Here a saw-like pattern is apparent in the emergence of new lineages across a variety of taxa since the early Cenozoic

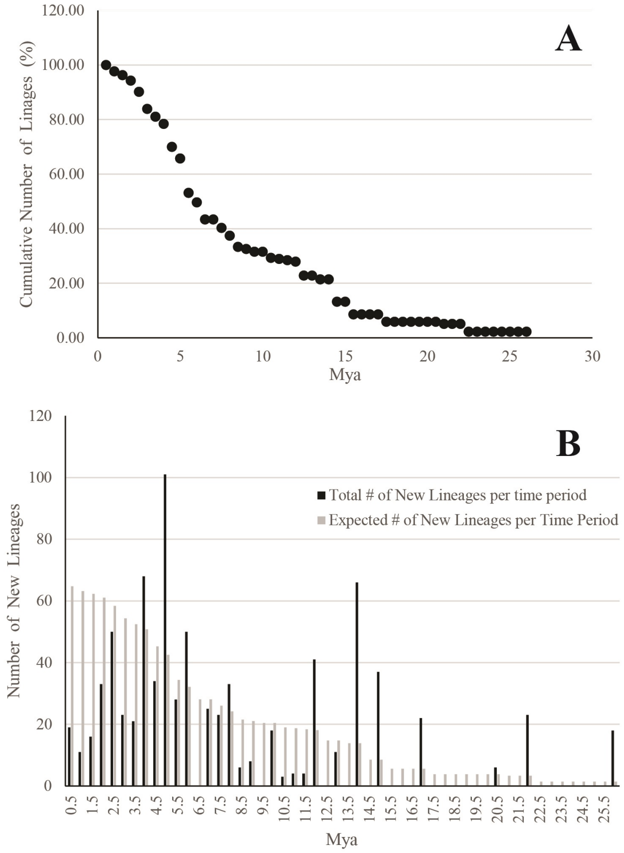

FIGURE 3 **(A)** Cumulative frequency of crown species development in the Amazon across a unbiased sampling of taxa from Rull (2008). The figure shows periods of stasis where no new lineages appeared punctuated by jumps corresponding with speciation pulses. These jumps are consistent with the predictions of the BDH. **(B)** Histogram of new lineages appearing in the last 26 My and the expected number of new lineages under the assumption of a uniform speciation rate based on the number of existing lineages. Data from Rull (2008).

with periods when new lineages are formed is alternated with periods where few, or no, lineages appeared. The positive correlations found constitute a statistical support of this pattern (Table 2). Lastly, Figure 6 shows global temperature from benthic deposits and indicates known glacial periods, the eustatic sea level, as well as the reported marine conditions in the Amazon basin. Marine conditions were not associated with warming periods during the Miocene or by raising sea levels, but rather the opposite. A clear trend of dropping temperatures prevails before and during marine conditions, which contradicts the notion that they resulted from marine incursions and supports a scenario in which the marine conditions developed in situ during dry periods.

DISCUSSION

A model of a mostly flooded continent with a mosaic of contracting and expanding habitats provides the conditions for abundant vicariant events across taxa and across most of the continent that may account for South America's high diversity. Since this process occurred only in South America, we have a system unique to South America that enhance the action of all known speciation processes which explains the much higher diversity found in South America compared with other tropical

TABLA 2 Spearman rank correlation of the appearance of new species among variety of South American lineages through the Cenozoic. The data from these correlation was obtained from Sigmodontine mice (Parada *et al.*, 2013), Army ants (Brady, 2003), Oven birds (Furnariidae) (Irestedt *et al.*, 2009), Attini ants (Ward *et al.*, 2015), Primates (Perelman *et al.*, 2011), Conopophagidae passerines (Batalha-Filho *et al.*, 2014), basal snakes (Colston *et al.*, 2013), armored catfish (Loricaridae) (Silva *et al.*, 2016), and piranhas (Serrasalmidae) (Thompson *et al.*, 2014). The dataset is provided in the supplementary material.* Denotes significance at 0.05 level, two-tails. ** Denotes significance at 0.01 level, two tails.

	(1)	**(2)**	**(3)**	**(4)**	**(5)**	**(6)**	**(7)**	**(8)**
(1) Sigmodontine	1.000							
(2) Dorylinae	-0.233	1.000						
(3) Conophaga	0.734**	-0.133	1.000					
(4) Furnaridae	0.599**	-0.257*	0.474**	1.000				
(5) Attini	-0.054	0.260*	-0.110	0.161	1.000			
(6) Boidae	0.039	0.100	0.088	0.021	-0.028	1.000		
(7) Platyrrhines	0.728**	-0.213	0.710**	0.715**	0.078	-0.045	1.000	
(8) Loricaridae	0.678**	-0.114	0.542**	0.694**	0.098	-0.033	0.740**	1.000
(9) Serrasalmidae	0.422**	0.058	0.528**	0.425**	0.135	0.008	0.385**	0.480**

continents (Fig. 1).

The fact that the appearance of new lineages is correlated with the height of the Andes, after removing the effect of the lineages present at the time, suggests that its high elevation is associated with the increase of diversity. The emergence of the Andes resulted in orogenic precipitation that may have increased flooding conditions (see below) and its effect on generating species pulses. Since the trade wins continued to bring moisture in to the continent but the high elevation of the Andes prevented this moisture from leaving the continent, the results would have been an increased in flooding as the Andes became taller; turning the continent into a sink of global water (Mörner *et al.*, 2016). Approximately 7 Mya, the Amazon acquired its current direction (Lundberg *et al.*, 1998; Hoorn *et al.*, 2010b). These would have produced substantial flooding and rearranging of new habitats, which would have increased the number of vicariant events in both terrestrial and aquatic systems. Consistent with the BDH, at this time the continent underwent a veritable explosion of new lineages across the continent spanning thousands of taxa and lasting until recent times (Fig. 3).

While the rise of the Andes would have also created a diversity of habitats along its altitudinal cline that would contribute to the increase of diversity (Ribas *et al.*, 2007), this effect would have been additive to the increase of vicariant events associated with the increase in flooding conditions. The influence of these two effects cannot be disentangled with the evidence presented here, but a mountain range's emergence producing new habitats associated with altitudinal clines has occurred in many other regions. Yet, only in the Andes did the rise of a mountain range produce the increase in diversity found in South America, suggesting that it is not only about the creation of new habitats or its environmental heterogeneity.

The appearance of new species seems to have a synchronous pattern —certainly in the modest number of taxa considered in this study (Figs. 3 and 4). The positive correlation found among the appearance of new taxa from different lineages is consistent with the idea that there were continent-wide (or at least region-wide) vicariant events that affected a variety of taxa. Contraction and expansion of habitats with small climatic fluctuations would explain the pattern found. It is intriguing that there is a positive correlation between of pulses speciation among endothermic with high mobility and aquatic taxa of vertebrates, but it does not seem to be present among ants or basal snakes. A possible explanation for this is that both

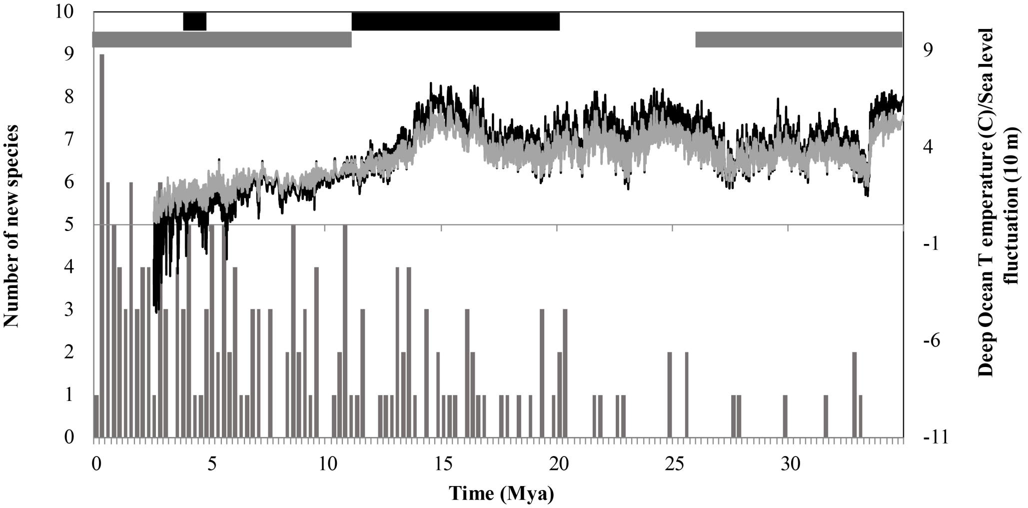

FIGURE 4 Number of new taxa appearance in the last 40 my in South America. Marine incursions alleged to have occurred (dark bars) (Lundberg *et al.*, 1998; Hovikoski *et al.*, 2010; Bloom & Lovejoy, 2011), presence of Antarctic ice sheet (grey bars), benthic oceanic temperature (grey line) obtained from (Zachos *et al.*, 2001, 2008), and eustatic sea levels divided by 10 for scaling (dark line) (Hansen *et al.*, 2013). Notice pulsating nature of the new taxa giving the graph a saw-like appearance.

birds and mammals have larger home ranges than snakes and ants Clearly birds can easily disperse over relatively extensive flooded areas. Recent studies with capuchin monkeys also show the they can disperse over relatively important rivers (Lima *et al.*, 2017). So, vicariant events for some of these taxa with less mobility may not have produced isolation among those taxa with higher mobility. This explains the lack of correlation among endotherms with high mobility and terrestrial ectotherms. A limitation of this approach is that the precision of the molecular clocks used to determine the appearance of new lineages is often in the millions of years and some of these vicariant events might have lasted much less than that. Yet, despite this limitation my results suggest a very strong trend. Clearly a more comprehensive survey of speciation processes across a variety of taxa, controlling for mobility, home range, and habitat would be needed to better understand this phenomenon.

Figure 4 shows no support for the notion of true marine incursions on the continent. The reported marine incursions did not occur during warming periods or during periods of sea level rise. Rather, there is a cooling trend throughout the last few million years that instead supports the notion of a drying world weather leading to marine conditions developing *in situ*. The question remains how marine conditions were corrected if the planet continued to cool after the marine conditions changed. There are two non-mutually exclusive explanations for this. One is that the changes in local climate brought more precipitation into the Guyanan and Brazilian shields. Their oligotrophic water would have diluted haline conditions developed in the basin. Alternatively, the continued rise of the Andes increased retention of water within the continent by developing orogenic precipitation (Mörner *et al.*, 2016). Losing less water to the Pacific Ocean via the trade winds would have diluted the marine conditions that had developed. With the continent now voiding its waters, and sediments, into the Atlantic Ocean, there is an outlet for the minerals responsible for the haline conditions at the continental level. Yet, salinas and salt water lagoons exist today in Mato Grosso do Sul in Brazil, which may well be relicts of these internal seas or perhaps analogous systems to them (Furquim *et al.*, 2010). The occurrence of saltwater conditions thousands of miles from the ocean provide definite prove that haline conditions may exist without a marine incursion and without drastic weather patterns.

Unfortunately, we do not have a good reconstruction of local and regional climatic patterns in South America's Miocene to see if the synchronic speciation among highly mobile vertebrates responds to local flooding events. However, the BDH allows us to hypothesize when they occurred. Figure 4 has the record of new species of birds and monkeys and allows for a concrete prediction. Speciation pulses of terrestrial species of high mobility should be associated with high water marks that isolated forest patches far enough to produce vicariant events among birds and monkeys (peaks of appearances of new species), while times of low appearance of new lineages were drier period when forest expanded (Fig. 4). In fact, due to how much water levels would have changed with a small difference in precipitation, I would expect the peaks of new lineage pulses to be far shorter and more frequent than what is implied in Fig. 3. As we develop better paleo-climatic models, better reconstruction of the paleo-climate of South America, and more finely timed phylogenies, we will be able to better explore these questions.

One of the strong evidences of marine transgressions comes from studies of fishes from marine clades that are present in the Amazon basin (Lovejoy & Albert, 2006). Of particular interest are Stingrays (Potamotrygonidae), since they are ubiquitous in the Amazon/Orinoco basin (de Carvalho & McEachran, 2003). The freshwater lineages show a split about 20 million years ago from their marine counterparts, shortly after the formation of the Pebas system. The authors argue that the vicariant event that split the lineages was immigration of a population of Stingrays during a marine incursion (Lovejoy, 1998). However, it is well known that Elasmobranchs venture freely into freshwater (de Carvalho & McEachran, 2003). An alternative explanation is that the vicariant event that split the lineages was a drought that prevented the Pebas system, at least partially, from draining into the Caribbean and thus interrupted gene flow between the continental and marine populations. In fact, if there was a marine transgression it is not clear why lineages would have split, if it all were ocean water. However, the isolation of an estuary from the ocean would have produced a real vicariant event. Figure 4 shows a drop in sea level at this time, which is not consistent with marine incursions, but rather a drier period. Furthermore, among the hypothesized drier periods in Figure 4 based on species pulse of primates and birds, there is precisely one that starts about 20 Mya when the "ocean transgression" was supposed to have started. Note that the prediction of this drier period is based on the speciation patterns of birds and monkeys, so these are independent lines of evidence for the presence of a dry period at this time, and they support the idea that the split of stingrays was due to dryer weather, rather than marine incursions. Salinity developed in situ does not necessarily explain better the presence of Marine Derive Lineages (MDLs) in the continent, but it explains it at least as well as the current interpretation and thus deserves further consideration. In addition, an estuary that connected to the sea and became disconnected in times of drought explains both the presence of Caribbean fish in the Amazon basin as well as Amazonian fishes in Miocene deposits of the Caribbean coast in current Venezuela (Lundberg & Aguilera, 2003).

Further evidence that MDLs present in South America descend from estuarine organisms that got trapped on the continent during continental droughts or sea level fall is the fact that the main MDLs found in South America are organisms that occur regularly in estuaries such as mangrove forest (Kathiresan & Bingham, 2001), foraminifera (Camacho *et al.*, 2015), seashells (Lima *et al.*), elasmobranchs as well as a variety of euryhaline fishes (Hubert & Renno, 2006; Lovejoy & Albert, 2006; Bloom & Lovejoy, 2011). If true ocean incursions in South America lasted as long as the marine incursions are supposed to have lasted, surely there would be fossils, or descendants, of strictly marine organisms present on the continent. However, all taxa found in South America are euryhaline organisms that regularly inhabit brackish and even fresh waters (Hubert & Renno, 2006; Lovejoy & Albert, 2006; Bloom & Lovejoy, 2011).

Marine incursions are a corner stone of fish biogeography in the South America. Saltwater bodies would act as barriers for freshwater fishes producing vicariant events leading to their speciation (Hubert & Renno, 2006). However, these explanations still hold under the BDH. The only difference is the source of the marine conditions. Hubert & Renno (2006) proposed freshwater refugia during these marine incursions that, not unlike Haffer's, were located toward the foothills of the Andes and the Guyanan and Brazilian shields where the marine waters could not reach. Under the BDH, the refuges remained freshwater because they received constant influx of fresh water from the higher watershed and drained their waters (and sediments) to the lower elevations, while the depressions in the low lands of the basin, that were not draining, became haline after accumulating enough sediments. In fact, the scenario of a system of salinity developing *in situ* better explains isolated marine conditions during the Acre system (in the current Acre state, Brazil) (Lundberg *et al.*, 1998) thousands of kilometers away from any sea entrance, or other marine conditions.

Furthermore, the notion that salt water developed *in situ*, explains the reports of “dilute marine incursions” (Wesselingh & Salo, 2006) as well as variable salinity reported in the Pebas system (Vonhof *et al.*, 1998; Wesselingh & Salo, 2006; Voelker *et al.*, 2013; Boonstra *et al.*, 2015; Jaramillo *et al.*, 2017). A drought that did not last very long would have resulted in brackish water, not a fully marine system. The variation in salinity in the Pebas system found in foraminifera deposits (Boonstra *et al.*, 2015) cannot be explained by an ocean transgression which would have brought in the same level of salinity across the area. However, variable contribution of different watersheds, and regional climatic differences in the basin, would have accounted for the variation in salinity. Input from the nutrient-rich Andes would have become haline faster than those from the oligotrophic Guyanan and Brazilian shields. This scenario also explains the high diversity of mollusk in the Pebas system (Wesselingh *et al.*, 2006; Wesselingh & Salo, 2006). Because calcium carbonate from mollusk shells has very high solubility in the acidic pH of black water, these waters would have been inhospitable for them. Expansion and contraction of black water bodies via variation in the relative contribution of each watershed would have produced speciation pulses contributing to the development of this high diversity.

Models using palynological signatures of the amazon sediments indicates that there was not a continuum rainforest in South America and they suggest that patches were separated by wedges of dry forest (Pennington *et al.*, 2000). However, studies of Net Primary Productivity (NPP) suggest the presence of highly productive ecosystems throughout which is incompatible with dry forest. Debate continues regarding the presence of large percentage of grasses (Poacea) in the palynological record that is often attributed to savannah. However, the pollen of aquatic grasses cannot be distinguished from dry land grasses (Mayle *et al.*, 2004). A scenario of large extensions of marshes and flooded aquatic habitat would account for the abundance of grasses without dry periods and with high NPP. This scenario explains all the existing, and seemingly contradictory, evidence.

Taken together, the study suggests that the Andes contributed to South America’s diversity via several mechanisms beyond what has been argued in terms of increasing habitat heterogeneity with its altitude, mainly by creating conditions for potentiated speciation processes. Vicariant events would be produced with the emergence of the Andes by (1) blocking the big river, flooding the continent producing dry land and aquatic systems, (2) retaining moisture from the trade winds and changing the climate that produced expansion and contraction of forest and aquatic ecosystems and, as the Andes range grew (3) large volumes of earthen crust that formerly had been under the ocean accumulated and the removal of such large volumes of crust would have contributed to eustatic drops of sea level (Miller *et al.*, 2005), where the drop in sea level isolated estuaries and river from the ocean and prevented freshwater ecosystems from voiding sediments, leading to haline conditions which in turn lead to more aquatic vicariant events.

While other authors have noted the correlation of the rise of the Andes and the increase of South American diversity, the mechanisms identified have been limited to biogeographic barrier, elevation gradients, and associated with nutrient and soil patchiness (Fine *et al.*, 2005; Ribas *et al.*, 2007, 2009; Quintero *et al.*, 2013). The impact of these explanations, though, is limited to few taxa and to the extreme western Amazon. The BDH provides a broader geographical effect that directly, and causally, explains South America’s high diversity across taxa. The BDH also explains the west to east diversity and moisture gradients (Cheng *et al.*, 2013; Crouch *et al.*, 2019; Oberdorff *et al.*, 2019), and west to east dispersal of new lineages (Bonaccorso *et al.*, 2006). Thus, rather than replace existing explanation for South America’s high diversity, the BDH provides a framework for the synergy of many of these explanation that is unique to South America.

The BDH also explains some of the questions that still elude explanation when we compare South America with other tropical continents. For instance, because it is unique to South America, it explains the greater Amazonian diversity than in either Africa or Asia. It also explains why South America is the only tropical continent without terrestrial primates. Extensions of patches of flooded forest would have been good habitat for tree dwelling primates but not ground dwelling ones. It explains the higher diversity of fresh water fishes in the Amazon and Orinoco basin (Albert *et al.*, 2011). A large flooded extension of a river that spills into the Caribbean very slowly is the perfect scenario for the great diversity of crocodilians (Langston, 1965; Salas-Gismondi *et al.*, 2015) and turtles (Cadena & Jaramillo, 2015) found in the Llanos/Magdalena basin. It also provides a scenario for the diversification of Boidae, producing strictly arboreal clades such as *Corallus* spp. as well as strictly aquatic ones such as *Titanoboa* spp. and *Eunectes* spp. (Noonan & Chippindale, 2006; Head *et al.*, 2009).

Furthermore, having large extensions of low-canopy flooded forest the likes of Varzea, Igapó, and isolated patches of Terra Firme explains the paucity of gliders. Gliding evolved repeatedly and in many taxa in the paleotropics, but there are surprisingly few of them in South America (Emmons & Gentry, 1983); despite its higher diversity across the board. If the tall trees were limited to a few scattered Terra Firme patches, gliding would not be very adaptive. Rather, powered flight would be far more useful. Being able to fly between isolated forest patches containing fruit trees, explains the magnificent explosive radiation of frugivorous microchiropetra we see in South America that has no equivalent anywhere else in the paleo-tropics (Teeling *et al.*, 2005; Lim, 2007).

CONCLUSIONS

Up to the present we have paid very little attention to the possible hydrographic and biogeographic repercussions of stopping the main drainage of a continent as moist and as flat as South America. While the Big Dam Hypothesis is speculative in nature, and its evidence is largely correlational, it does provide an internally consistent model for the synergistic action of multitude of speciation processes that explains all the current evidence as well as, or better than, the accepted models. Most importantly, it takes into consideration the hydrological consequences of damming one of the largest rivers of the Tertiary, which other models have failed to consider. Because it applies to a broad variety of taxa across the continent, it has the potential to provide an overarching process explaining the South America's high diversity and thus deserves further scrutiny. Hopefully future studies will support or falsify the fundamentals of this hypothesis.

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CONFLICTS OF INTEREST

The author declare no conflicts of interest.

SUPPLEMENTARY MATERIAL

Appendix S1. Original data and statistical analyses used to develop this study. Information could be directly downloaded at: http://erevistas.saber.ula.ve/index.php/ecotropicos/article/view/E0014/21921927720

RESUMEN

Cambios climáticos y pulsos de especiación en un continente semi-inundado: atacando el misterio de la alta diversidad de Sur América. Entender el origen de la diversidad biológica de Sur América es especialmente importante hoy, en vista a nuestras crisis de extinción mundial de cara al cambio climático. Aunque ha habido mucho debate sobre el origen de la alta diversidad de Sur América, no hay consenso sobre un proceso general que afecta todo el continente y variedad de taxa. En esta contribución, presento un modelo teórico considerando el impacto del tectonismo e hidrología en la historia del continente. Cuando los Andes se levantaron, represó el rio Paleo-Amazonas, que corría hacia el oeste. Esto produjo una inundación generalizada en todo el continente en donde los bosques estaban en las áreas más elevadas rodeados de hábitats inundados. Debido al relieve plano de la hoya Amazónica, pequeños cambios en el nivel de agua hubieran resultado en expansión y contracción de bosques, produciendo pulsos de especiación. En este estudio analizo datos de la literatura en distribución de especies, y de la edad de nuevos linajes usando estudios moleculares. Muestro que los procesos de especiación en tiempo y espacio corresponden con las predicción es del modelo en el continente. Este modelo también postula que no hubo incursiones marinas en Sur America y que las condiciones marinas que se han encontrado en la historia del continente se hubieran desarrollado *in situ*.

Palabras clave: Amazonas, biodiversidad, macroevolución, paleo-ecología, especiación.

REFERENCIAS

Albert JS, Petry P & Reis RE. **2011**. Major biogeographic and phylogenetic patterns. *Historical biogeography of Neotropical freshwater fishes* **1**: 21–57.

Antonelli A, Zizka A, Carvalho FA, Scharn R, Bacon CD, Silvestro D & Condamine FL. **2018**. Amazonia is the primary source of Neotropical biodiversity. *Proceedings of the National Academy of Sciences of the United States of America* **115**: 6034–6039.

Archer AW. **2005**. Review of Amazonian depositional systems. In: **Blum M, Marriot S & Leclair S** (Eds.) *Fluvial sedimentology VII.*, Blackwell Publishing Ltd, Kingston-upon-Thames, UK, pp. 17–39.

Armstrong KE, Stone GN, Nicholls JA, Valderrama Escallón E, Anderberg AA, Smedmark J, Gautier L, Naciri Y, Milne R & Richardson JE. **2014**. Patterns of diversification amongst tropical regions compared: A case study in Sapotaceae. *Frontiers in Genetics* **5**: 116–129.

Batalha-Filho H, Pessoa RO, Fabre PH, Fjeldså J, Irestedt M, Ericson PG, Silveira LF & Miyaki CY. **2014**. Phylogeny and historical biogeography of gnateaters (Passeriformes, Conopophagidae) in the South America forests. *Molecular Phylogenetics and Evolution* **79**: 422–432.

Bicudo TC, Sacek V, de Almeida RP, Bates JM & Ribas CC. **2019**. Andean tectonics and Mantle Dynamics as a Pervasive Influence on Amazonian ecosystem. *Scientific reports* **9**: 1–11.

Bloom DD & Lovejoy NR. **2011**. The Biogeography of Marine Incursions in South America. In: **Albert JS & Reis RE** (Eds.) *Historical Biogeography of Neotropical Freshwater Fishes*, University of California Press, Berkley, USA, pp. 137–144.

Bonaccorso E, Koch I & Peterson AT. **2006**. Pleistocene fragmentation of Amazon species' ranges. *Diversity and Distributions* **12**: 157–164.

Boonstra M, Ramos M, Lammertsma E, Antoine PO & Hoorn C. **2015**. Marine connections of Amazonia: Evidence from foraminifera and dinoflagellate cysts (early to middle Miocene, Colombia/Peru). *Palaeogeography, Palaeoclimatology, Palaeoecology* **417**: 176–194.

Brady SG. **2003**. Evolution of the army ant syndrome: the origin and long-term evolutionary stasis of a complex of behavioral and reproductive adaptations. *Proceedings of the National Academy of Sciences* **100**: 6575–6579.

Bush MB. **1994**. Amazonian Speciation: a necessarily complex model. *Journal of Biogeography* **21**: 5–17.

Bush MB & Oliveira PE. **2006**. The rise and fall of the Refugial Hypothesis of Amazonian speciation: a paleoecological perspective. *Biota Neotropica* **6**: bn00106012006.

Cadena E & Jaramillo C. **2015**. Early to middle Miocene turtles from the northernmost tip of South America: giant testudinids, chelids, and podocnemidids from the Castilletes Formation, Colombia. *Ameghiniana* **52**: 188–203.

Camacho S, Moura D, Connor S, Scott D & Boski T. **2015**. Ecological zonation of benthic foraminifera in the lower Guadiana Estuary (southeastern Portugal). *Marine Micropaleontology* **114**: 1–18.

Carrillo L, Palacios-Hernández E, Yescas M & Ramírez-Manguilar AM. **2009**. Spatial and seasonal patterns of salinity in a large and shallow tropical estuary of the Western Caribbean. *Estuaries and Coasts* **32**: 906–916.

Cheng H, Sinha A, Cruz FW, Wang X, Edwards RL, D'Horta FM, Ribas CC, Vuille M, Stott LD & Auler AS. **2013**. Climate change patterns in Amazonia and biodiversity. *Nature Communications* **4**: 1411.

Claramunt S & Cracraft J. **2015**. A new time tree reveals Earth history's imprint on the evolution of modern birds. *Science advances* **1**: e1501005.

Colinvaux P & De Oliveira P. **2001**. Amazon plant diversity and climate through the Cenozoic. *Palaeogeography, Palaeoclimatology, Palaeoecology* **166**: 51–63.

Colinvaux PA, Oliveira PE & Bush MB. **2000**. Amazonian and neotropical plant communities on glacial time-scales: The failure of the aridity and refuge hypotheses. *Quaternary Science Reviews* **19**: 141–169.

Colston TJ, Grazziotin FG, Shepard DB, Vitt LJ, Colli GR, Henderson RW, Hedges SB, Bonatto S, Zaher H, Noonan BP *et al.* **2013**. Molecular systematics and historical biogeography of tree boas (*Corallus* spp.). *Molecular Phylogenetics and Evolution* **66**: 953–959.

Cordeiro-Bicudo T, Sacek V, de Almeida RP, Bates JM & Ribas CC. **2019**. Andean tectonics and Mantle Dynamics as a Pervasive Influence on Amazonian ecosystem. *Scientific Reports* **9**: 1–11.

Crouch NM, Capurucho JM, Hackett SJ & Bates JM. **2019**. Evaluating the contribution of dispersal to community structure in Neotropical passerine birds. *Ecography* **42**: 390–399.

Daly DC & Mitchell JD. **2000**. Lowland vegetation of tropical South America–an overview. In: **Lentz D** (Ed.) *Imperfect balance: landscape transformations in the pre-Columbian Americas*, Columbia University Press, New York, USA, pp. 391–454.

De Aguiar MA, Baranger M, Baptestini EM, Kaufman L & Bar-Yam Y. **2009**. Global patterns of speciation and diversity. *Nature* **460**: 384–387.

de Carvalho MR & McEachran JD. **2003**. Family Carcharhinidae (requiem sharks) . In: **Reis RE, Kullander SO & Ferraris CJ** (Eds.) *Check List of the Freshwater Fishes of South and Central America*, Edipucrs, Porto Alegre, Brazil, pp. 13–16.

Duellman WE. **1982**. Quaternary climatic-ecological fluctuations in the lowland tropics: frogs and forests. In: **Prance GT** (Ed.) *Biological Diversification in the Tropics*, Columbia University Press, New York, USA, pp. 389–402.

Díaz de Gamero MLD. **1996**. The changing course of the Orinoco River during the Neogene: a review. *Palaeogeography, Palaeoclimatology, Palaeoecology* **123**: 385–402.

Emmons LH & Gentry AH. **1983**. Tropical forest structure and the distribution of gliding and prehensile-tailed vertebrates. *The American Naturalist* **121**: 513–524.

Erwin T & Adis J. **1982**. Amazonian inundation forest: their role as short term refuges and generators of species richness and taxon pulses. In: **Prance GT** (Ed.) *Biological Diversification in the Tropics*, Columbia University Press, New York, USA, pp. 358–371.

Ferreira LV, de Almeida SS, Parolin P *et al.* **2010**. Amazonian white-and blackwater floodplain forests in Brazil: large differences on a small scale. *Ecotropica* **16**: 31–41.

Fine PA, Daly DC & Cameron KM. **2005**. The contribution of edaphic heterogeneiyt to the evolution and diversity of burseracear trees in the western Amazon. *Evolution* **59**: 1464–1478.

Fjeldså J. **1994**. Geographical patterns for relict and young species of birds in Africa and South America and implications for conservation priorities. *Biodiversity and Conservation* **3**: 207–226.

Furquim SAC, Graham RC, Neto JPQ & Vidal-Torrado P. **2010**. Soil mineral genesis and distribution in a saline lake landscape of the Pantanal Wetland, Brazil. *Geoderma* **154**: 518–528.

Garzione CN, Hoke GD, Libarkin JC, Withers S, MacFadden B, Eiler J, Ghosh P & Mulch A. **2008**. Rise of the Andes. *Science* **320**: 1304–1307.

Gregory-Wodzicki KM. **2000**. Uplift history of the Central and Northern Andes: a review. *Geological Society of America Bulletin* **112**: 1091–1105.

Guedes TB, Sawaya RJ, Zizka A, Laffan S, Faurby S, Pyron RA, Bernils RS, Jansen M, Passos P, Prudente AL *et al.* **2018**. Patterns, biases and prospects in the distribution and diversity of Neotropical snakes. *Global Ecology and Biogeography* **27**: 14–21.

Haffer J. **1969**. Speciation in Amazonian forest birds. *Science* **131**: 131–137.

Haffer J. **1982**. General aspects of the refuge theory. In: **Prance GT** (Ed.) *Biological diversification in the tropics*, Columbia University Press, New York, USA, pp. 6–24.

Haffer J. **1992**. On the "river effect" in some forest birds of southern Amazonia. *Boletin del Museum Para Emilio Goeldi serie Zoologica* **8**: 217–245.

Haffer J. **2008**. Hypotheses to explain the origin of species in Amazonia. *Brazilian Journal of Biology* **68**: 917–947.

Haffer J & Prance GT. **2001**. Climatic forcing of evolution in Amazonia during the Cenozoic: On the refuge theory of biotic differentiation. *Amazoniana* **16**: 579–607.

Hansen J, Sato M, Russell G & Kharecha P. **2013**. Climate sensitivity, sea level and atmospheric carbon dioxide. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences* **371**: 20120294.

Hayes F & Sewlal JA. **2004**. The Amazon River as a dispersal barrier to passerine birds : effects of river width , habitat and taxonomy. *Journal of Biogeography* **31**: 1809–1818.

Head JJ, Bloch JI, Hastings AK, Bourque JR, Cadena EA, Herrera FA, Polly PD & Jaramillo CA. **2009**. Giant boid snake from the Palaeocene neotropics reveals hotter past equatorial temperatures. *Nature* **457**: 715–717.

Honorio Coronado EN, Dexter KG, Pennington RT, Chave J, Lewis SL, Alexiades MN, Alvarez E, Alves de Oliveira A, Amaral IL, Araujo-Murakami A *et al.* **2015**. Phylogenetic diversity of Amazonian tree communities. *Diversity and Distributions* **21**: 1295–1307.

Hoorn C. **2006**. Mangrove forests and marine incursions in Neogene Amazonia (lower Apaporis River, Colombia). *Palaios* **21**: 197–209.

Hoorn C, Bogotá-A GR, Romero-Baez M, Lammertsma EI, Flantua SG, Dantas EL, Dino R, do Carmo DA & Chemale Jr F. **2017**. The Amazon at sea: Onset and stages of the Amazon River from a marine record, with special reference to Neogene plant turnover in the drainage basin. *Global and Planetary Change* **153**: 51–65.

Hoorn C, Guerrero J, Sarmiento GA & Lorente MA. **1995**. Andean tectonics as a cause for changing drainage patterns in Miocene northern South America. *Geology* **23**: 237–240.

Hoorn C, Wesselingh F, Ter Steege H, Bermudez M, Mora A, Sevink J, Sanmartín I, Sanchez-Meseguer A, Anderson C, Figueiredo J *et al.* **2010**a. Amazonia through time: Andean uplift, climate change, landscape evolution, and biodiversity. *Science* **330**: 927–931.

Hoorn C, Wesselingh FP, Hovikoski J, Guerrero J *et al.* **2010**b. The development of the amazonian mega-wetland (Miocene; Brazil, Colombia, Peru, Bolivia). In: **Hoorn C & Wesselingh F** (Eds.) *Amazonia, landscape and species evolution: a look into the past*, Hoboken: Blackwell-Wiley, West Sussex, UK, pp. 123–142.

Hovikoski J, Wesselingh FP, Räsänen M, Gingras M & Vonhof HB. **2010**. Marine influence in Amazonia: evidence from the geological record. In: **Hoorn C & Wesselingh F** (Eds.) *Amazonia, landscape and species evolution: a look into the past*, Hoboken: Blackwell-Wiley, West Sussex, UK, pp. 143–161.

Hubbell SP. **2001**. *The unified neutral theory of biodiversity and biogeography (MPB-32).* Princeton University Press, New Jersey, USA.

Hubert N & Renno JF. **2006**. Historical biogeography of South American freshwater fishes. *Journal of Biogeography* **33**: 1414–1436.

Humboldt AV. **1850**. *Views of Nature or the contemplation on the sublime phenomena of creation* . Harrison and Sons, London.

IBM Corp. **2011**. IBM SPSS Statistics for Windows.

Irestedt M, Fjeldså J, Dalén L & Ericson PG. **2009**. Convergent evolution, habitat shifts and variable diversification rates in the ovenbird-woodcreeper family (Furnariidae). *BMC evolutionary biology* **9**: 268.

IUCN. **2017**. The IUCN red list of threatened species. Disponible en: https://www.iucnredlist.org/. (Consultado el 22 de Mayo de 2020).

Jackson ND & Austin CC. **2010**. The combined effects of rivers and refugia generate extreme cryptic fragmentation within the common ground skink (*Scincella lateralis*). *Evolution: International Journal of Organic Evolution* **64**: 409–428.

Janzen D. **1976**. Why are there so many species of insects? In: **Whit D** (Ed.) *Proceedings of the XV International Congress of Entomology*, The Entomological Society of America, Washington D.C, USA, pp. 84–94.

Jaramillo C, Romero I, D'Apolito C, Bayona G, Duarte E, Louwye S, Escobar J, Luque J, Carrillo-Briceño JD, Zapata V *et al.* **2017**. Miocene flooding events of western Amazonia. *Science Advances* **3**: e1601693.

Kathiresan K & Bingham BL. **2001**. Biology of mangroves and mangrove ecosystems. *Advances in Marine Biology* **40**: 84–254.

Langston JW. **1965**. Fossil crocodilians from Colombia and the Cenozoic history of the Crocodilia in South America. *University of California Publications in Geological Sciences* **52**: 1–157.

Latimer AW, Silander JA & Cowling RM. **2001**. Neutral ecological theory reveals isolation and rapid speciation in a biodiversity hotspot. *Science* **309**: 1722–1725.

Latrubesse EM, Cozzuol M, da Silva-Caminha SA, Rigsby CA, Absy ML & Jaramillo C. **2010**. The Late Miocene paleogeography of the Amazon Basin and the evolution of the Amazon River system. *Earth-Science Reviews* **99**: 99–124.

Leigh Jr EG, Davidar P, Dick CW, Terborgh J, Puyravaud JP, ter Steege H & Wright SJ. **2004**. Why do tropical forest have so many species of trees? *Biotropica* **36**: 447–473.

Leite YL, Costa LP, Loss AC, Rocha RG, Batalha-Filho H, Bastos AC, Quaresma VS, Fagundes V, Paresque R, Passamani M *et al.* **2016**. Neotropical forest expansion during the last glacial period challenges refuge hypothesis. *Proceedings of the National Academy of Sciences* **113**: 1008–1013.

Lim BK. **2007**. Divergence times and origin of neotropical sheath-tailed bats (Tribe Diclidurini) in South America. *Moleculuar Phylogenetics and Evolution* **45**: 777–791.

Lima MG, Buckner JC, Silva-Júnior JdSe, Aleixo A, Martins AB, Boubli JP, Link A, Farias IP, da Silva MN, Röhe F *et al.* **2017**. Capuchin monkey biogeography: understanding *Sapajus* Pleistocene range expansion and the current sympatry between *Cebus* and *Sapajus*. *Journal of Biogeography* **44**: 810–820.

Lima SFB, Lucena RA, Santos GM, Souza JW, Christoffersen ML, Guimarães CR & Oliveira GS. 2017. Inventory of mollusks from the estuary of the Paraíba River in northeastern Brazil. *Biota Neotropica* **17**: e20160239.

Lovejoy NR. **1998**. Marine incursion into South America. *Nature* **396**: 421–422.

Lovejoy NR & Albert JS. **2006**. Miocene marine incursions and marine/freshwater transitions: Evidence from Neotropical fishes. *Journal of South American Earth Sciences* **21**: 5–13.

Lundberg JG & Aguilera O. **2003**. The Late Miocene *Phractocephalus* catfish (Siluriformes: Pimelodidae) from Urumaco, Venezuela: additional specimens and reinterpretation as a distinct species. *Neotropical Ichtyology* **1**: 97–109.

Lundberg JG, Marshall LG, Guerrero J, Horton B, Malabarba MCSL & Wesselingh F. **1998**. The stage for Neotropical fish diversification: A history of tropical South American rivers. In: **Malabarba L, Reis RE, Vari RP, Lucena ZMS & Lucena CAS** (Eds.) *Phylogeny and Classification of Neotropical Fishes*, Edipucrs, Porto Alegre, pp. 13–48.

Mayle FE, Beerling DJ, Gosling WD & Bush MB. **2004**. Responses of Amazonian ecosystems to climatic and atmospheric carbon dioxide changes since the last glacial maximum. *Philosophical Transactions of the Royal Society B: Biological Sciences* **359**: 499–514.

Miller KG, Kominz MA, Browning JV, Wright JD, Mountain GS, Katz ME, Sugarman PJ, Cramer BS, Christie-Blick N & Pekar SF. **2005**. The Phanerozoic record of global sea-level change. *Science* **310**: 1293–1298.

Mittermeier RA, Mittermeier CG, Pilgrim J, Fonseca G & Konstant WR. **2002**. The pantanal - Wilderness: Earth's last wild places. In: **Mittermeier RA, Mittermeier CG, Pilgrim J, Fonseca G & Konstant WR** (Eds.) *Wilderness: Earth's last wild places (No. 333.782 W673w)*, México, MX: CEMEX, Mexico D.F., Mexico, pp. 246–263.

Molino JF & Sabatier D. **2001**. Tree diversity in tropical rain forests: a validation of the intermediate disturbance hypothesis. *Science* **294**: 1702–1704.

Mora A, Baby P, Roddaz M, Parra M, Brusset S, Hermoza W & Espurt N. **2010**. Tectonic history of the Andes and sub-Andean zones: implications for the development of the Amazon drainage basin. In: **Hoorn C & Wesselingh F** (Eds.) *Amazonia, landscape and species evolution: a look into the past*, Hoboken: Blackwell-Wiley, West Sussex, UK, pp. 38–60.

Moritz C, Patton JL, Schneider CJ & Smith TB. **2000**. Diversification of rainforest faunas: an integrated molecular approach. *Annual Review of Ecology and Systematics* **31**: 533–563.

Morlon H. **2014**. Phylogenetic approaches for studying diversification. *Ecology Letters* **17**: 508–525.

Mörner NA *et al.* **2016**. Origin of the Amazonian rainforest. *International Journal of Geosciences* **7**: 470–478.

Naka LN & Brumfield RT. **2018**. The dual role of Amazonian rivers in the generation and maintenance of avian diversity. *Science advances* **4**: eaar8575.

Noonan BP & Chippindale PT. **2006**. Dispersal and vicariance: the complex evolutionary history of boid snakes. *Molecular Phylogenetics and Evolution* **40**: 347–358.

Oberdorff T, Dias MS, Jézéquel C, Albert JS, Arantes CC, Bigorne R, Carvajal-Valleros FM, De Wever A, Frederico RG, Hidalgo M *et al.* **2019**. Unexpected fish diversity gradients in the Amazon basin. *Science Advances* **5**: eaav8681.

Parada A, Pardiñas UF, Salazar-Bravo J, D'Elía G & Palma RE. **2013**. Dating an impressive Neotropical radiation: molecular time estimates for the Sigmodontinae (Rodentia) provide insights into its historical biogeography. *Molecular phylogenetics and Evolution* **66**: 960–968.

Pennington T, Prado DE & Pendry CA. **2000**. Neotropical seasonally dry forests and Quaternary vegetation changes. *Journal of Biogeography* **27**: 261–273.

Perelman P, Johnson WE, Roos C, Seuánez HN, Horvath JE, Moreira MA, Kessing B, Pontius J, Roelke M, Rumpler Y *et al.* **2011**. A molecular phylogeny of living primates. *PLoS Genet* **7**: e1001342.

Pianka ER. **1977**. Latitudinal gradients in species diversity: a review of concepts. *The American Naturalist* **100**: 33–46.

Pires J & Prance G. **1985**. The vegetation types of the Brazilian Amazon. In: **Prance GT & Lovejoy TE** (Eds.) *Key Environments: Amazonia*, Pergamon Press, Oxford, UK, pp. 109–145.

Prance GT. **1979**. Notes on the vegetation of Amazonia III. The terminology of Amazonian forest types subject to inundation. *Brittonia* **31**: 26–38.

Prance GT. **1982**. *Biological Diversification in the Tropics*. Columbia University Press, New York, USA.

Quintero E, Ribas CC & Cracraft J. **2013**. The Andean *Hapalopsittaca* parrots (Psittacidae, Aves): An example of montane-tropical lowland vicariance. *Zoologica Scripta* **42**: 28–43.

Ribas CC, Aleixo A, Nogueira AC, Miyaki CY & Cracraft J. **2012**. A palaeobiogeographic model for biotic diversification within Amazonia over the past three million years. *Proceedings of the Royal Society B: Biological Sciences* **279**: 681–689.

Ribas CC, Miyaki CY & Cracraft J. **2009**. Phylogenetic relationships, diversification and biogeography in Neotropical *Brotogeris* parakeets. *Journal of Biogeography* **36**: 1712–1729.

Ribas CC, Moyle RG, Miyaki CY & Cracraft J. **2007**. The assembly of montane biotas: linking Andean tectonics and climatic oscillations to independent regimes of diversification in *Pionus* parrots. *Proceedings of the Royal Society B: Biological Sciences* **274**: 2399–2408.

Rivas RA, Mittermeier CG, Pilgrim J, Fonseca G & Konstant WR. **2002**. The llanos. In: **Mittermeier RA, Mittermeier CG, Pilgrim J, Fonseca G & Konstant WR** (Eds.) *Wilderness: Earth's last wild places (No. 333.782 W673w)*, México, MX: CEMEX, Mexico D.F., Mexico, pp. 265–273.

Roddaz M, Brusset S, Baby P & Hérail G. **2006**. Miocene tidal-influenced sedimentation to continental Pliocene sedimentation in the forebulge–backbulge depozones of the Beni–Mamore foreland Basin (northern Bolivia). *Journal of South American Earth Sciences* **20**: 351–368.

Roxburgh SH, Shea K & Wilson JB. **2004**. The intermediate disturbance hypothesis: patch dynamics and mechanisms of species coexistence. *Ecology* **85**: 359–371.

Rull V. **2008**. Speciation timing and neotropical biodiversity: The Tertiary-Quaternary debate in the light of molecular phylogenetic evidence. *Molecular Ecology* **17**: 2722–2729.

Rull V. **2011**. Neotropical biodiversity: timing and potential drivers. *Trends in Ecology & Evolution* **26**: 508–513.

Rull V. **2015**. Pleistocene speciation is not refuge speciation. *Journal of Biogeography* **42**: 602–604.

Salas-Gismondi R, Flynn JJ, Baby P, Tejada-Lara JV, Wesselingh FP & Antoine PO. **2015**. A Miocene hyperdiverse crocodylian community reveals peculiar trophic dynamics in proto-Amazonian mega-wetlands. *Proceedings of the Royal Society B: Biological Sciences* **282**: 20142490.

Santos JC, Coloma LA, Summers K, Caldwell JP, Ree R & Cannatella DC. **2009**. Amazonian amphibian diversity is primarily derived from Late Miocene Andean lineages. *PLoS Biology* **7**: e1000056.

Sayer EJ, Sutcliffe LM, Ross RI & Tanner EV. **2010**. Arthropod abundance and diversity in a lowland tropical forest floor in Panama: the role of habitat space *vs*. nutrient concentrations. *Biotropica* **42**: 194–200.

Schoener TW. **1971**. Large-billed insectivorous birds: a precipitous diversity gradient. *The Condor* **73**: 154–161.

Sepulchre P, Sloan LC & Fluteau F. **2010**. Modelling the response of Amazonian climate to the uplift of the Andean mountain range. In: **Hoorn C & Wesselingh F** (Eds.) *Amazonia, landscape and species evolution: a look into the past*, Hoboken: Blackwell-Wiley, West Sussex, UK, pp. 211–222.

Silva GS, Roxo FF, Lujan NK, Tagliacollo VA, Zawadzki CH & Oliveira C. **2016**. Transcontinental dispersal, ecological opportunity and origins of an adaptive radiation in the Neotropical catfish genus *Hypostomus* (Siluriformes: Loricariidae). *Molecular Ecology* **25**: 1511–1529.

Strecker M, Alonso R, Bookhagen B, Carrapa B, Hilley G, Sobel E & Trauth M. **2007**. Tectonics and climate of the southern central Andes. *Annual Review of Earth and Planetary Sciences* **35**: 747–787.

Teeling EC, Springer MS, Madsen O, Bates P, O'Brien SJ & Murphy WJ. **2005**. A molecular phylogeny for bats illuminates biogeography and the fossil record. *Science* **307**: 580–584.

Terborgh J. **1992**. Maintenance of diversity in tropical forests. *Biotropica* **24**: 283–292.

Terborgh J, Robinson SK, Parker III TA, Munn CA & Pierpont N. **1990**. Structure and organization of an Amazonian forest bird community. *Ecological Monographs* **60**: 213–238.

Terborgh J & Weske JS. **1975**. The role of competition in the distribution of Andean birds. *Ecology* **56**: 562–576.

Thompson AW, Betancur-R R, López-Fernández H & Ortí G. **2014**. A time-calibrated, multi-locus phylogeny of piranhas and pacus (Characiformes: Serrasalmidae) and a comparison of species tree methods. *Molecular Phylogenetics and Evolution* **81**: 242–257.

Valle-Levinson A & Bosley KT. **2003**. Reversing circulation patterns in a tropical estuary. *Journal of Geophysical Research: Oceans* **108**: 3331.

Voelker G, Marks BD, Kahindo C, A'genonga U, Bapeamoni F, Duffie LE, Huntley JW, Mulotwa E, Rosenbaum SA & Light JE. **2013**. River barriers and cryptic biodiversity in an evolutionary museum. *Ecology and Evolution* **3**: 536–545.

Vonhof H, Wesselingh F, Kaandorp R, Davies G, Van Hinte J, Guerrero J, Rasanen M, Romero-Pittman L & Ranzi A. **2003**. Paleogeography of Miocene Western Amazonia: Isotopic composition of molluscan shells constrains the influence of marine incursions. *Geological Society of America Bulletin* **115**: 983–993.

Vonhof HB & Kaandorp RJ. **2010**. Climate variation in Amazonia during the Neogene and the Quaternary. In: **Hoorn C & Wesselingh F** (Eds.) *Amazonia, landscape and species evolution: a look into the past*, Hoboken: Blackwell-Wiley, West Sussex, UK, pp. 201–210.

Vonhof HB, Wesselingh FP & Ganssen GM. **1998**. Reconstruction of the Miocene Western Amazonian aquatic system using molluscan isotopic signatures. *Palaeogeography, Palaeoclimatology, Palaeoecology* **141**: 85–93.

Ward PS, Brady SG, Fisher BL & Schultz TR. **2015**. The evolution of myrmicine ants: phylogeny and biogeography of a hyperdiverse ant clade (Hymenoptera: Formicidae). *Systematic Entomology* **40**: 61–81.

Weir JT. **2006**. Divergent Timing and Patterns of Species Accumulation in Lowland and Highland Neotropical Birds. *Evolution* **60**: 842–855.

Wesselingh F, Anderson L & Kadolsky D. **2006**. Molluscs from the Miocene Pebas Formation of Peruvian and Colombian Amazonia. *Scripta Geologica* **133**: 19–290.

Wesselingh F & Salo J. **2006**. A Miocene perspective on the evolution of the Amazonian biota. *Scripta Geologica* **133**: 439–458.

Wesselingh FP & Hoorn C. **2011**. Geological development of Amazon and Orinoco basins. In: **Albert JS & Reis RE** (Eds.) *Historical Biogeography of Neotropical Freshwater Fishes*, University of California Press, Berkely, Los Angeles, USA, pp. 59–67.

Zachos J, Pagani M, Sloan L, Thomas E & Billups K. **2001**. Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science* **292**: 686–693.

Zachos JC, Dickens GR & Zeebe RE. **2008**. An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics. *Nature* **451**: 279–283.