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Review article

The changing course of the Amazon River in the Neogene: center stage for Neotropical diversification

James S. Albert¹, Pedro Val^{2,3} and Carina Hoorn⁴

We review geological evidence on the origin of the modern transcontinental Amazon River, and the paleogeographic history of riverine connections among the principal sedimentary basins of northern South America through the Neogene. Data are reviewed from new geochronological datasets using radiogenic and stable isotopes, and from traditional geochronological methods, including sedimentology, structural mapping, sonic and seismic logging, and biostratigraphy. The modern Amazon River and the continental-scale Amazon drainage basin were assembled during the late Miocene and Pliocene, via some of the largest purported river capture events in Earth history. Andean sediments are first recorded in the Amazon Fan at about 10.1-9.4 Ma, with a large increase in sedimentation at about 4.5 Ma. The transcontinental Amazon River therefore formed over a period of about 4.9-5.6 million years, by means of several river capture events. The origins of the modern Amazon River are hypothesized to be linked with that of mega-wetland landscapes of tropical South America (*e.g.* várzeas, pantanals, seasonally flooded savannahs). Mega-wetlands have persisted over about 10% northern South America under different configurations for >15 million years. Although the paleogeographic reconstructions presented are simplistic and coarse-grained, they are offered to inspire the collection and analysis of new sedimentological and geochronological datasets.

Keywords: Biostratigraphy, Geochronology, Landscape Evolution Model, River capture, Transcontinental Amazon.

Este trabalho é uma revisão das evidências geológicas sobre a origem do moderno rio Amazonas transcontinental, e a história paleogeográfica das conexões ribeirinhas entre as principais bacias sedimentares do norte da América do Sul durante o Neógeno. São revisados novos conjuntos de dados geocronológicos usando isótopos radiogênicos e estáveis, e de métodos geocronológicos tradicionais, incluindo sedimentologia, mapeamento estrutural, exploração sísmica e bioestratigrafia. O atual rio Amazonas e sua bacia continental se formaram durante o final do Mioceno e do Plioceno, através de alguns dos maiores eventos de captura de rio na história da Terra. Os sedimentos andinos são registrados pela primeira vez no leque fluvial do Amazonas por volta de 10,1-9,4 Ma, com um grande aumento na sedimentação a cerca de 4,5 Ma. O rio Amazonas transcontinental, portanto, se formou durante um período de cerca de 4,9 a 5,6 milhões de anos, por meio de vários eventos de captura de rios. Acredita-se que as origens do moderno rio Amazonas estejam ligadas às paisagens de inundação da América do Sul tropical (por exemplo, várzeas, pantanais, savanas sazonalmente inundadas). As áreas pantanosas persistiram em cerca de 10% do norte da América do Sul sob diferentes configurações por mais de 15 milhões de anos. Embora as reconstruções paleogeográficas apresentadas sejam simplistas, elas são oferecidas para inspirar a coleta e análise de novos conjuntos de dados sedimentológicos e geocronológicos.

Palavras-chave: Amazonas transcontinental, Bioestratigrafia, Captura de rio, Geocronologia, Modelos de evolução de paisagem.

Introduction

The principle of uniformitarianism avers “the present is the key to the past”, asserting the universality of natural laws and processes across space and through time. This principle is a pillar of the historical sciences, upon which rest modern practices in the fields of geomorphology, paleontology and biogeography (Simpson, 1963; Stanley, 1979; Shea, 1982).

In these sciences the reverse is also often just as important, where the current state of a geological or biological system can only be fully understood in light of conditions as they were in the past (Webb *et al.*, 2002; Fine, Ree, 2006; Kissling *et al.*, 2012; Albert, Antonelli, 2017). Celebrated examples from biogeography include the biotic assemblages of the southern continents following the breakup of Gondwana (Cracraft, 1973; Linder, Crisp, 1995; Lundberg *et al.*, 1998;

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Sparks, Smith, 2004), the Greater Antilles by means of co-ordinated dispersal under the influence of geographically persistent dispersal vectors (Iturralde-Vinent, MacPhee, 1999; Tagliacollo *et al.*, 2017), and the response of the North American biota to Pleistocene ice-age cycles (Webb, 1977; Knouft, Page, 2003; Pielou, 2008).

Nowhere on Earth does history play a more important role in understanding the coevolution of landscape and life than in Greater Amazonia, a biodiversity province that extends over 8.4 million km² of Amazon and Orinoco lowlands and adjacent portions of the Guiana and Brazilian Shields (Albert *et al.*, 2011a; Reis *et al.*, 2016; Van der Sleen, Albert, 2017). The Amazon rainforest ecosystem and Amazon drainage basin are the largest of their respective kinds on Earth, being home to one of the greatest concentrations of species diversity on the planet (Wallace, 1889; Pimm *et al.*, 2014). Most Amazonian plant and animal lineages have ancient origins in the super-greenhouse world of the Late Cretaceous (100-66 Ma) and Paleogene (66-23 Ma), and the biota achieved approximately modern dimensions during the Neogene (23-2.6 Ma; Lundberg *et al.*, 1998; Antonelli *et al.*, 2009, 2010; Albert *et al.*, 2011b; López-Fernández, Albert, 2011). In general, continental-scale systems like the Amazon rainforest and drainage basin do not form all at once, but rather accumulate under the influence of numerous contributing factors over periods of millions of years.

The great drainage basins of tropical northern South America (NSA) were assembled during the Neogene, during which time many important geographic features of the modern world assumed their modern configurations (Potter, Hamblin, 2006; Potter, Szatmari, 2009; Horton, 2017). These include formation of the modern latitudinal climate regimes (Knorr, Lohmann, 2003), world's tallest mountain ranges (*e.g.* Alps, Andes, Himalayas, etc.), and largest river systems (*e.g.* Amazon, Orinoco, Brahmaputra, Congo, Danube, Yangtze; Courtillot *et al.*, 2003; Potter, Szatmari, 2009). As with all these drainages, the present-day Amazon formed by the process of *river capture* (Goudie, 2005; Ashworth, Lewin, 2012; Winn *et al.*, 2017; Albert *et al.*, 2018). River capture is a geomorphological process (*sensu* Gilchrist, Summerfield, 1991; Bishop, 2007) operating perennially on most continental surfaces, whereby a portion of one river basin is diverted into a different drainage, thereby moving the watershed boundary between the two basins. River capture alters connectivity patterns among portions of river networks through time (Bishop, 1995; Brookfield, 1998; Albert, Crampton, 2010; Willett *et al.*, 2014) and, as a consequence, affects evolutionary diversification in obligate riverine taxa by separating and merging segments of drainage networks (Wilkinson *et al.*, 2010; Albert *et al.*, 2017).

The effects of river capture on speciation and extinction are complex and intertwined. By subdividing species geographic ranges river capture isolates populations on either side of a new watershed divide, thereby promoting speciation. However, because these isolated populations have smaller population sizes, river capture can serve to

increase extinction risk. Yet curiously, river capture can also inhibit the processes of speciation and extinction by facilitating dispersal (*i.e.* geographic range expansion) among populations in newly merged river segments. As a result of these complex effects, river capture has been implicated in the formation of high freshwater diversity in many regions and taxa (see review in Albert *et al.*, 2018). River capture has contributed substantially to diversification in many aquatic and terrestrial Amazonian taxa that are ecologically restricted to rivers, floodplains, and riparian woodlands (*e.g.* Aleixo, 2004; Albert *et al.*, 2006; Lovejoy *et al.*, 2010; Albert, Carvalho, 2011; Ribas *et al.*, 2012; Roxo *et al.*, 2014; Tagliacollo *et al.*, 2015). The role of river capture in biotic diversification has also been demonstrated in many other regions of the world (Stanford, Ward, 1993; Robinson *et al.*, 2002; Ward *et al.*, 2002; BurrIDGE *et al.*, 2006; Smith *et al.*, 2010; Carrea *et al.*, 2014; Craw *et al.*, 2016).

As with many of Earth's ancient tropical biotas (*e.g.* Wiens, Donoghue, 2004; Cowman, Bellwood, 2011), most of the species-rich Amazonian clades and ecosystems are older than the geographic conditions in which they live today (Hoorn *et al.*, 2010a, 2010b; Albert *et al.*, 2011a; Graham, 2011). Although the precise age of the modern west-to-east-flowing transcontinental Amazon River system is still incompletely understood, the main events are estimated to have occurred in the Neogene. Published age estimates for the origin of the transcontinental Amazon range over two orders of magnitude, from 0.1 to 12.6 Ma (Tab. 1). These dates have been estimated from a variety of geochronological, sedimentological and paleontological studies, using data obtained from drill cores, outcrops, and wells located in the Amazon and Orinoco basins, and from offshore sites in the Amazon Fan and Ceará Rise, an oceanic ridge east of the Amazon River mouth (*e.g.* Dobson *et al.*, 2001; Figueiredo *et al.*, 2009, 2010; Heinrich, Zonneveld, 2013; Hoorn *et al.*, 2017). Fig. 1 illustrates the major sources of sediment types delivered to the mouth of the Amazon, and Fig. 2 provides a summary of information from sedimentary cores located near the mouth of the Amazon.

Beginning in the 1990s, Hoorn and colleagues advanced a general timeline in which the modern transcontinental Amazon was assembled by means of an extraordinarily large mega river capture event during the late Miocene (c. 11-9 Ma; see Hoorn, 1993; Hoorn *et al.*, 1995; Lundberg *et al.*, 1998; Wesselingh, Hoorn, 2010). A mega-capture is a river capture event involving more than 1,000 km², or about 0.29° latitude and longitude at the equator (Albert *et al.*, 2018), a spatial scale that is expected to affect third-order streams and larger, and therefore rates of net lineage diversification in obligate riverine taxa (Tedesco *et al.*, 2012). This mega-capture event is the largest of its kind ever proposed, transferring approximately 1,600,000 km² of watershed area from the sub-Andean foreland to the eastern Amazon (Albert *et al.*, 2018). The capture process involved diverting Caribbean-draining basins of the Western Amazon into the Atlantic-draining Eastern Amazon, and a concomitant

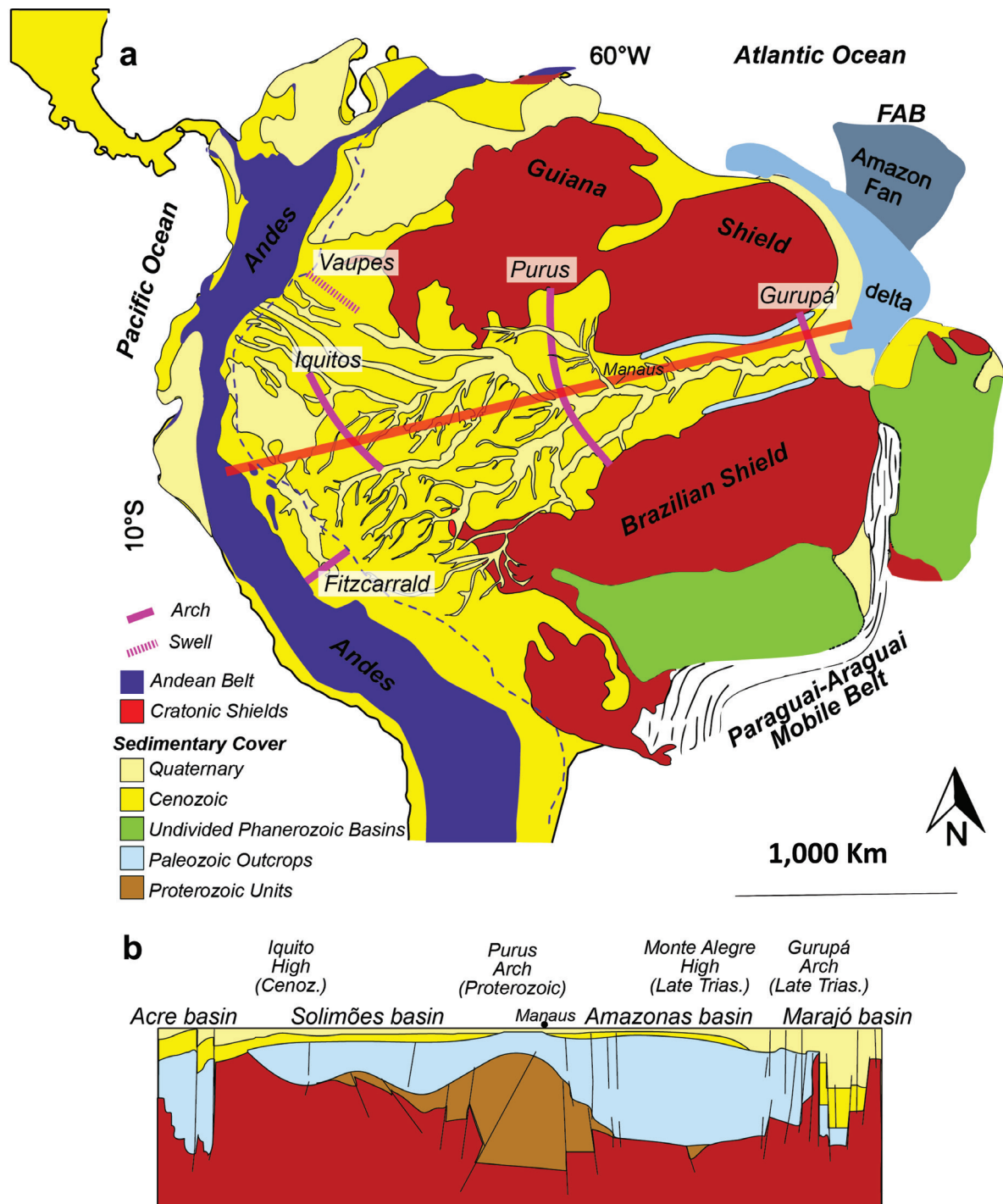


Fig. 1. Geological map of northern South America. **a.** Geological units that formed the provenance area for the sediment input into the Amazon subaqueous delta and submarine fan (adapted from Hoorn *et al.*, 2017). FAB, Foz do Amazonas Basin. **b.** Schematic longitudinal section (orange bar) of the Amazon river basin showing sedimentary basins and structural arches (adapted from Wanderley-Filho *et al.*, 2010; Caputo, Soares 2016).

separation of western Amazonian basins from the Orinoco basin by the rise of the Vaupés Arch (Mora *et al.*, 2010). This river capture event diverted Andean waters to flow eastwards across the whole of northern South America and into the Atlantic, depositing Andean-derived sediments at or near the mouth of the modern Amazon River.

The formation of the transcontinental river system occurred by breaching or transgression of the Purús Arch, a subsurface high with Paleozoic origins, which is formed part of the eastern watershed or margin of the sub-Andean foreland during the Cretaceous and Paleogene (Mora *et al.*, 2010; Wanderley-Filho *et al.*, 2010; Hurtado *et al.*, 2018; see also

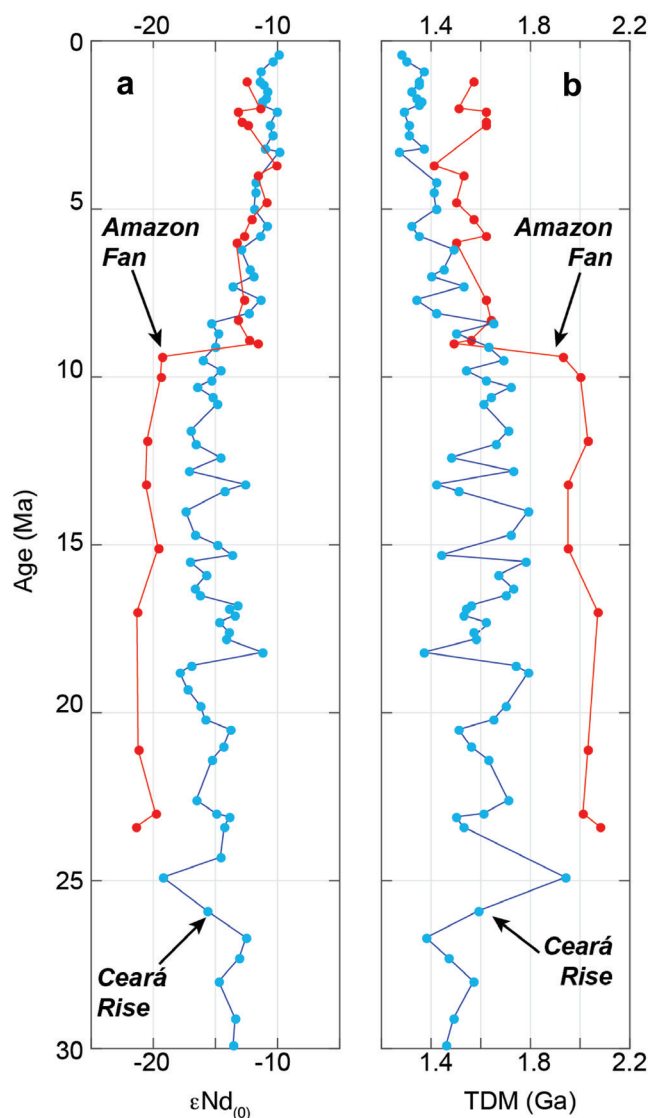


Fig. 2. Summary of terrigenous signals from drilling cores near the mouth of the Amazon River. Sediment dating of cores in the Amazon Fan (red; Hoorn *et al.*, 2017) and Ceará Rise (blue; van Soelen *et al.*, 2017). **a.** Ratios of stable Neodymium isotopes expressed in epsilon notation: $\epsilon\text{Nd}(0)$. **b.** Crustal residence times (τDM). Note values of both parameters change through time according to the provenance of the preserved terrigenous material. $\epsilon\text{Nd}(0) < -15$ and a $\tau\text{DM} > 1.67$ Ga reflect a primarily cratonic source. Both the Amazon Fan and Ceará Rise record significant changes away from a cratonic source (towards an Andean source) by c. 9-7 Ma.

below). Understanding the precise timing and sequence of this geomorphological event, contributing to the formation of the expansive Amazon catchment, is of central concern to the study of Neotropical biodiversity (Cracraft, 1985; Lundberg, 1998; Tedesco *et al.*, 2005; Hoorn *et al.*, 2010a; Albert *et al.*, 2011; Antonelli, Sanmartín, 2011; Dias *et al.*, 2014; Smith *et al.*, 2014). Constraining age estimates on the

origin of the transcontinental Amazon River informs models on the diversification of taxa with geographic ranges that extend over large areas of Greater Amazonia. Some phylogenetic studies of avian and mammalian genera have recovered Pliocene (5.3-2.6 Ma) divergence times among deeper branches, leading to the hypothesis that these events were associated with, or even caused by, the onset of the transcontinental Amazon River in the last 2.5 My (*e.g.* Ribas *et al.*, 2012; Sousa-Neves *et al.*, 2013; Fernandes *et al.*, 2014; Alfaro *et al.*, 2015). Studies on other taxa (fishes, amphibians, some birds, plants) have recovered late Miocene (10-5 Ma) dates for divergences among clades that inhabit multiple sedimentary basins of Amazonia (*e.g.* Antonelli *et al.*, 2009, 2010; Santos *et al.*, 2009; Albert *et al.*, 2011a; Tagliacollo *et al.*, 2015; Carneiro *et al.*, 2018).

This paper has three main goals. The first is to explicate the role of sedimentary basins, bounded by uplands and structural arches, as fundamental geological units constraining the evolution of river basins in NSA through the Neogene. The second goal is to describe the spatial and temporal dimensions of a multi-stage model for the origin of the modern transcontinental Amazon River (*sensu* Figueiredo *et al.*, 2009; Hoorn *et al.*, 2017). The third goal is to describe the formation of mega-wetland landscapes in Greater Amazonia, a series of seasonally flooded várzeas and savannas that extend over more than one million square kilometers across tropical NSA (Miguez-Macho, Fan, 2012). The results support a pluralist approach to the study of basin and landscape evolution, in which multiple processes contribute to the formation of continental-scale river basins (Potter, 1978; Goudie, 2005; Potter, Hamblin, 2006; Hoorn *et al.*, 2017; van Soelen *et al.*, 2017), and the evolutionary diversification of riverine-associated taxa at continental scales (Santos *et al.*, 2009; Albert *et al.*, 2011a, 2017; Ribas *et al.*, 2018).

Geological setting of Northern South America. “Although most of the stocks passed through periods in which they inhabited the eastern highlands, it was not until the Amazon developed its great freshwater basin that it became the greatest hatchery of species known (Eigenmann, Allen, 1942: 62).”

This section provides a brief primer of key terms, concepts, and geological features used in studies on the geomorphology and geology of the Amazon basin. Readers familiar with these issues may wish to skip ahead to the next section.

The principal landforms controlling the evolution of rivers in NSA are the upland Guiana and Brazilian Shields, the Andes, and a set of structural arches and sedimentary depositional basins, all of heterogeneous geological origins (Fig. 3). Many of these geological features have been known since the early 20th Century (Schuchert, 1906; Branner, 1919), and some have been documented and characterized only in recent years.

The Guiana and Brazilian Shields, referred to collectively by Carl Eigenmann as the “eastern highlands”, form, respectively, the northern and southern margins of Central

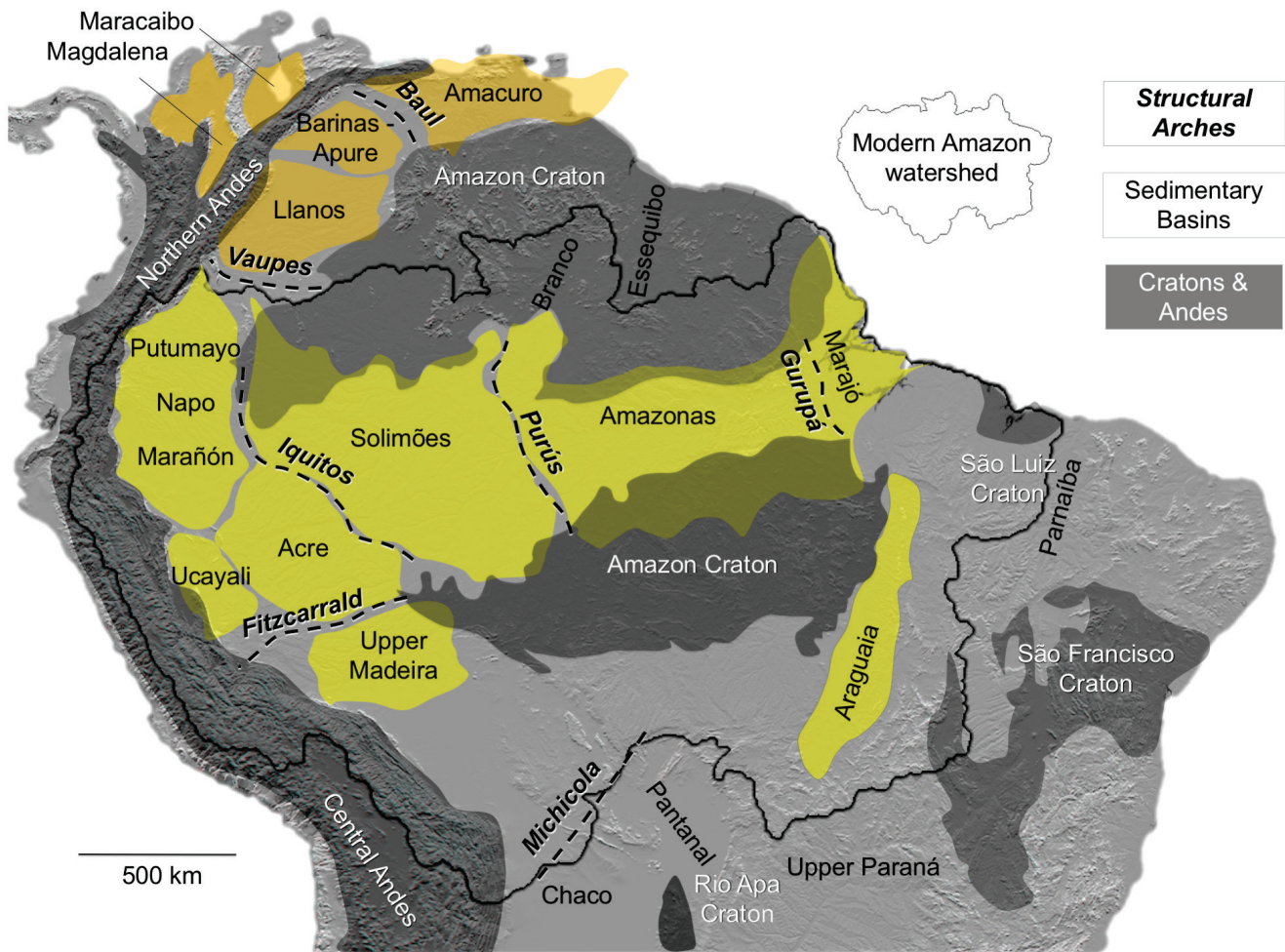


Fig. 3. Principle landforms controlling basin connectivity in northern South America. Structural arches (dashed lines) of diverse geological origins partially bounding sedimentary basins. Sedimentary basins in orange draining to the Caribbean; in yellow to the Atlantic. Structural arches and sedimentary basins from Costa Menegazzo *et al.* (2016) and Jaramillo *et al.* (2017). Note the Guiana Shield is composed mostly of the northern Amazon Craton, the Brazilian Shield by the southern Amazon craton, and the Atlantic Shield by the São Luís, São Francisco, Luís Alves and Río de la Plata cratons, all overlaid in parts with Paleozoic sedimentary formations.

and Eastern Amazon drainage basin in Brazil. These shields are now known to be composed of Proterozoic (2,500–541 Ma) crystalline igneous and metamorphic rocks that form the Amazon craton, along with some overlying Paleozoic (541–252 Ma) sedimentary formations (Hartmann, 2002). Together the shield regions occupy a total of ~4.1 million km², or about 46% of the total area of NSA.

The much younger Andes orogenic belt extends along the western margin of the continent as a series of parallel and transverse ranges (cordilleras), plateaus and depressions. The Andes formed during the Late Cretaceous and Cenozoic (100–0 Ma) by compression and mountain building along the western margin of South America (Barckhausen *et al.*, 2008; Horton, 2017). Subduction on the western South American margin drove a transition from an extensional tectonic regime associated with a westward (Pacific) draining pre-Andean landscape, to a compressive regime with an eastward (Atlantic) draining landscape during the Late

Cretaceous and Paleogene (Louterbach *et al.*, 2018). The highlands of the Northern and Central Andes occupy an area of ~1.6 million km², or about 18% the area of NSA.

The remaining ~3.3 million km² or about 36% of NSA are lowland sedimentary basins, generally below about 250–300 m elevation. These lowland basins are drained by thousands of kilometers of large and deep (>5 m mid-channel depth) rivers meandering and anastomosing across broad sunlit floodplains, and tens of thousands of kilometers of non-floodplain (*terra firme*) streams and rivers, many flowing mostly under a closed-forest canopy (Toivonen *et al.*, 2007; Crampton, 2011).

Many faces of the Amazon. The term *Amazon* describes several different and overlapping hydrological, geological, biological, and political entities. To avoid confusion, it is useful to distinguish the use of the term *Amazon* as the name of a drainage basin, river, biodiversity province, and ecoregion. The *Amazon drainage basin* is a watershed circumscribing

more than 7.05 million km² (including the Tocantins-Araguaia drainage basins), collecting waters from across 40% of the entire continental surface of South America, or about 5.2% the surface area of all river basins on Earth combined (Lehner *et al.*, 2008). This immense catchment is the most expansive drainage basin documented, and given that the continents are today larger than in previous eras (Hawkesworth *et al.*, 2013), the Amazon drainage may be among the greatest ever assembled in Earth history (Albert *et al.*, 2018). The Amazon drainage more-completely dominates South America than any other river basin on the planet, having accrued more than 42% of the total continental river-space, as compared with, for example, 24% by the Mississippi, 14% by the Yangtze, or 12% by the Congo drainages (Lehner *et al.*, 2008).

Drawing water from this tremendous area, the *Amazon River* has the greatest annual flow on Earth, discharging an average of about 219,000 m³ s⁻¹ or 20% of the world's total river water delivered to the sea, an amount greater than the next nine largest rivers of the world combined (Nittrouer, DeMaster, 1986; Milliman, 2001). The Amazon River also contains the largest surface area of wetlands (*c.* 250,000 km²), seasonally-inundated floodplains, savannahs, inland estuaries, and forests that may be flooded for many months of the annual cycle (Goulding *et al.*, 2003; Gupta, 2007; Jongman *et al.*, 2008; Melak, Hess, 2010). The use of the term *Amazon* as a drainage and river must not be confused with the *Amazon sedimentary basin*, a geological depression of about 620,000 km² that lies between the Brazilian and Guiana Shields, and between the Purús and Gurupá structural arches (described in more detail below).

The Amazon drainage basin collects waters from across much of *Greater Amazonia*, a vast and ecologically heterogeneous biodiversity province, including alpine streams and torrential rivers of the Northern and Central Andes, moist lowland rainforests and seasonally-inundated floodplains, and seasonally-burned savannahs of the Guiana and Brazilian uplands shields. The margins of Greater Amazonia broadly coincide with that of the *Amazon Rainforest* ecoregion, the largest contiguous region of moist, tropical forests on Earth. This ecoregion covers about 5,500,000 km² in nine countries, including most of lowland Amazonia, but excluding non-forested ecoregions of the Llanos in the Orinoco drainage, and the upper reaches of major rivers in the Brazilian Shield (*e.g.* Upper Madeira, Tapajos, Xingu, Tocantins).

The term *Amazon* is also used in the official names of states or departments in four nations; Brazil (1,570,745 km²), Colombia (109,665 km²), Peru (39,249 km²), and Venezuela (183,500 km²). In units of political geography, a majority of the Amazon drainage basin lies in Brazil (4,756,680 km² or 67%), with large areas also in Bolivia (836,628 km² or 12%), Colombia (610,265 km² or 9%), Ecuador (92,000 km² or 1%), Peru (549,522 km² or 8%), and Venezuela (183,500 km² or 3%).

Rivers, basins and arches. In describing the evolution of drainage networks, geomorphologists distinguish between several distinct uses of the term “*basin*” (Einsele, 1992;

Monroe, Wicander, 1997; Lambert, 1998). A “*drainage basin*”, also called catchment or watershed, is a hydrological term for a land surface area in which all precipitation is contained within the watershed domain, either evaporating (or evapotranspiring), infiltrating into soil, and/or flowing to streams and eventually reaching the main stem. By contrast, a “*structural basin*” is a geological term for a large-scale topographic depression formed by tectonic deformation. Many structural basins are also “*sedimentary basins*”, regions of the Earth surface with long-term subsidence and/or large accommodation space, where sediments accumulate and are preserved over geological time periods. Subsidence in turn often results from flexure of the crust due to topographic (caused by tectonics) or sedimentary (caused by erosion of uplifting highlands) loading (*e.g.* Jordan, 1981), but can also result from other processes as well, such as a downward, cold mantle flow underneath the Earth's crust (*e.g.* Forte *et al.*, 1993). These processes act over different spatial and temporal scales and lead to distinct basin architectures. Active tectonics (*i.e.* plate collision), flexure, mantle flow, and intraplate faulting are all processes that cause or caused subsidence in different locations in the Amazon region and controlled the formation of its major sedimentary basins (*e.g.* Shephard *et al.*, 2010; Wanderley-Filho *et al.*, 2010; Eakin *et al.*, 2014; Sacek, 2014; Caputo, Soares, 2016).

From a biogeographic perspective, a river may usefully be perceived as a whole drainage basin (*e.g.* Abell *et al.*, 2008; Dagosta, de Pinna, 2017; Tedesco *et al.*, 2017). The English word “*river*” (and cognates in many Indo-European languages, including the Spanish “*rio*” and Portuguese “*rio*”) derive from Latin “*ripa*” for “*bank*”, indicating that a river is defined by its banks. However, insightful observers have emphasized the fluid nature of rivers; *e.g.* *panta rhei* or “*everything flows*” by Heraclites of Ephesus (Robinson, 1987). The modern conception of a river includes waterways with multiple channels, those with intermittent or ephemeral flow, bankless waterways like the Florida Everglades or Pantanal Matogrossense, and the baseflow of groundwater from the watershed or catchment watertable (Ritter *et al.*, 1995; Wiens, 2002; Pimentel, Hamza, 2012). The river channel contains only the subaerial portion of the total basin discharge. Channel flow contributes substantially to the total erosion of a continental hydrological system (Willenbring *et al.*, 2013) and strongly affects important features of aquatic habitats like channel and floodplain morphology in the Amazon basin (Crampton, 2011). However, the sub-flow of groundwater contributes substantially to basin-wide erosion, in particular to headwater erosion, and therefore to the movement of watershed boundaries (Schaller, Fan, 2009; Miguez-Macho, Fan, 2012).

From a geomorphological perspective, a drainage system develops from a hierarchy of water flux processes occurring over a range of spatial and temporal scales, under particular geographic settings and particular climatic regimes (Goudie, 2005; Conti, 2012). Fluvial and erosional processes range from local hydraulic and sediment movement processes of

channels operating over daily or annual time scales, to basin-scale processes associated with regional geological and global climatological contexts operating over millions of years. All the sediment stored in basins ultimately derives from a parent rock source. Fluvial erosion of the highlands (*i.e.* Andes and, to a lower extent, cratons) operating over millennia in response to regional geological processes (*i.e.* uplift of the Andes) is responsible for most of the sediment being transported and deposited downstream. Once caught in the fluvial system, sediments in large basins such as the Amazon may undergo several cycles of transportation and burial until reaching its ultimate “sink”, the ocean basin (*e.g.* Wittmann *et al.*, 2011).

It is not possible to describe the geologic setting of the sedimentary basins in Amazonia without describing their bounding structures, the structural arches. A “*structural arch*” or swell is a surface or sub-surface high or positive feature caused by relative uplift over an elongated region. The main structural arches in the Amazon drainage region are the Iquitos (or Envira), Purús, and Gurupá arches (Horbe *et al.*, 2013). It is often observed that hard basement rock (or sometimes consolidated sediments) form parts of the boundary between adjacent sedimentary depositional basins (Wanderley-Filho *et al.*, 2010). Such inter-basin arches may form under the influence of several different geological processes. Localized uplift may arise from tectonic subduction (*e.g.* Fitzcarrald and Vaupés Arches), oroclinal bending (*e.g.* Michicola Arch), forearc bulges (*e.g.* El Baul and Iquitos Arches), or strike-slip faults (*e.g.* Gurupá Arch). Structural arches can be reflected in the surface topography if there is differential subsidence and sediment deposition along adjacent fault zones (*e.g.* Michicola Arches). When expressed in the surface topography, structural arches form topographic barriers to drainage basins.

The Purús Arch is the portion of the Ventuari-Tapajos igneous belt that is today entirely buried under Neogene sediments of the modern transcontinental Amazon River (see fig. 1 in Bahlburg *et al.*, 2009). The Ventuari-Tapajos belt is the one of four NW/SE trending geochronological provinces of Proterozoic origin that constitute the Amazon Craton, the belts decreasing in age from northeast to southwest (Cordani, Sato, 1999). The Ventuari-Tapajos belt formed during the Paleoproterozoic (*c.* 2.0-1.82 Ga) as igneous granitoids in a continental arc margin setting (Payolla *et al.*, 2002). Given its great age, the Purús Arch has undergone a complex geological history (Wanderley-Filho, 1991; Bahlburg *et al.*, 2009; Johansson, 2009; Caputo *et al.*, 2016; Merdith *et al.*, 2017). The Purús Arch originally formed as an inverted graben by NW-SE compression of the Amazon Craton during the Neoproterozoic (*c.* 1000-541 Ma), became exposed as a persistent structural high until the Pennsylvanian (*c.* 300 Ma), underwent multiple episodes of subsidence and uplift during the Permian, Triassic and Jurassic (*c.* 300-145 Ma), was again a sustained topographic high throughout the Cretaceous and most of the Cenozoic (*c.* 145-10 Ma), and became buried by Andean-derived sediments with the onset of

the modern transcontinental Amazon River.

Using the terms as defined above, we can better understand the geological setting of Northern South America (Fig. 1). The Amazon basin is not a rift valley, or even a single geological depression. Rather, the Amazon drainage basin is composed of four larger, and several smaller, structural basins, each encompassing one or more geologically distinct sedimentary basins, and all separated from one another by structural arches. The main axis of the Amazon River drains a series of sedimentary basins that formed over a protracted interval during much of the Phanerozoic (541-0 Ma). Most of these sedimentary basins formed in association with tectonic rifting of the South American and Africa plates during the Lower Cretaceous (145-100 Ma), and all these sedimentary basins were affected by uplift of the northern Andes during the Paleogene and Neogene. Broadly speaking, patterns of sediment dispersal and accumulation, and drainage reorganization in NSA reflect landscape evolution associated with protracted subduction of the Farallon, Nazca, and Cocos Plates (Horton, 2017). The underlying geological mechanisms can be traced to tectonic uplifts of the Northern Andes that occurred in several distinct orogenic phases, called the Incaic (48-34 Ma), Quechua 1 (17-15 Ma), Quechua 2 (9-8 Ma), and Quechua 3 (7-5 Ma) Phases (Gregory-Wodzicki, 2000; Pfiffner, Gonzalez, 2013; Bermúdez *et al.*, 2015; Chiarabba *et al.*, 2016; Horton, 2017).

The Western Amazon region encompasses several sub-Andean sedimentary basins (*e.g.* Acre, Marañón), while the Solimões, Amazonas, and Marajó sedimentary basins are intracratonic basins. Andean-derived fluvial sediments are recorded in the sub-Andean foreland from at least the early Paleocene or Eocene (Hurtado *et al.*, 2018). The Western Amazon also separated from the Llanos basin to the north by the Vaupés Arch, and from the Upper Madeira basin in the south by the Fitzcarrald Arch. The Solimões and Amazonas basins are bounded to the north and south by portions of the Amazon Craton, represented as Guiana Shield to the north and Central Brazilian (or Guaporé Shield) to the south.

Recent studies emphasize the complex and diachronous (time-varying) uplift and deformation history of the northern Andes among its several parallel cordilleras and along its latitudinal extent (Garzzone *et al.*, 2017). While orogenesis (mountain building) is the underlying process that leads to massive erosion and sedimentation in the adjacent basins, later sediment redistribution and landscape changes might have been at least partly controlled by mantle-convection processes affecting the South American plate (Shephard *et al.*, 2010), flat slab subduction (Eakin *et al.*, 2014), and progressive eastward sediment-load driven flexure of the lithosphere (Sacek 2014).

Palaeodrainage history of NSA. “The key to the long-term survival of a large river is location on a long-lived craton or passive margin and persistence of continental tilt, all without interruption by desertification, continental glaciation or volcanism (Potter, Hamblin, 2006: 1).”

Here we present a model of palaeodrainage evolution among the sedimentary basins of NSA, based on geochronological data obtained from multiple data types and sources (Sternberg, 1950; Potter, 1997; Lundberg *et al.*, 1998; Costa *et al.*, 2001; Hoorn *et al.*, 2010a, 2017; Roddaz *et al.*, 2010; Horton *et al.*, 2015a; 2015b; Anderson *et al.*, 2016; Horton, 2017; van Soelen *et al.*, 2017; Hurtado *et al.*, 2018). This model describing the origin of the modern Amazon and adjacent river basins has only come into focus in the past several decades (Hoorn *et al.*, 1995; Díaz de Gamero, 1996; Lundberg *et al.*, 1998; Hoorn *et al.*, 2010a, 2017). Although we do not have space here to summarize all the alternative models proposed in the literature regarding the timing and configuration of these events, citations relevant to this literature are provided in Tab. 1. The data summarized in this paper are consistent with many but not all of these models.

Early studies from terrestrial sources based primarily on stratigraphic, structural mapping and macrofossil data (*e.g.* Frailey *et al.*, 1988; Campbell *et al.*, 2001) estimated Pliocene dates for the onset of the modern transcontinental Amazon (Tab. 1). By contrast, studies using isotopes and sediment geochemistry obtained from marine sediments off the coast of NE Brazil, early (*e.g.* Dobson, 1997, 2001) and consistently (*e.g.* Figueiredo *et al.*, 2009, 2010; Gorini *et al.*, 2014) estimated late Miocene dates. More recent studies combining data from multiple data types (including terres-

trial pollen and marine plankton fossils, mass spectrometry, electron paramagnetic resonance spectroscopy) and regions (terrestrial and marine) have concluded late Miocene dates for the origin of the modern Amazon drainage regime (Caputo, Soares, 2016; Hoorn *et al.*, 2017; Jaramillo *et al.*, 2017; van Soelen *et al.*, 2017; Allard *et al.*, 2018; Lammertsma *et al.*, 2018).

Studies based on the optically stimulated luminescence (OSL) dating method have reported Pleistocene (2.6-0.01 Ma) dates for the onset of transcontinentalization (Rossetti *et al.*, 2015; Cremon *et al.*, 2016). In our view, interpreting these dates, orders of magnitude younger than dates obtained using other methods, is clouded by several concerns. OSL measures a luminescence signal trapped in a crystalline lattice due to ambient radiation (*i.e.* the surrounding sediments) as an estimate of the amount of time an object has been shielded from sunlight. The technique was originally developed to date ceramics and other objects with crystalline structures (bones, shells) from archeological sites, and is competent for objects up to several hundreds of thousands of years old, beyond which the signal becomes saturated (Murray, Olley, 2002; Rhodes, 2011; Roberts *et al.*, 2015; Wintle, Adamiec, 2017).

These Pleistocene dates estimated from OSL studies of Amazonian sediments are enigmatic. These dates may derive in part from quartz crystals that were exhumed at superficial incisions of a deeper sedimentary pile, as incision dates

Tab. 1. Summary of literature age estimates for onset of transcontinental Amazon river. Studies arranged by descending order of estimated mega-river capture date. Data types: Geophysics includes data from fission track (FT), radiometric (RM), stable isotopes (SI), and optical luminescence (OL). Sedimentology includes sediment provenance from stratigraphy, lithology, and chemistry (ST), structural mapping (SM), sonic or seismic logging (SL), and sedimentation or subsidence rates (SR). Biostratigraphy includes planktonic microfossils (PM), pollen (PO), and macrofossils (MF). Regions: Ama, Amazonas basin; Atl, Atlantic (Amazon fan, Ceará rise); Lla, Llanos basin; NSA, Northern South America; Sol, Solimões basin; Wam, Western Amazon basins. Data sources are terrestrial (Ter) or marine (Mar).

Epoch	Dates	Reference	Data type(s)			Region(s)	Source(s)
	Ma		Geochronology	Sedimentol.	Biostrat.		
Upper Miocene	12.6	Jaramillo <i>et al.</i> , 2017	SI (13C)	ST, SL	PM, PO, MF	Lla, Wam	Mar. & Ter.
	11.6 – 11.2	Heinrich, Zonneveld, 2013		ST, SR	PM	Atl	Mar.
	10.5	Figueiredo <i>et al.</i> , 2010	RM, SI (Sm-Nd)	ST, SL	PM	Atl	Mar.
	10.1	Caputo, Soares, 2016	ST*, SL*, SI* (U-Pb)	ST*, SM*		NSA	Mar. & Ter.
	10.1	Mora <i>et al.</i> , 2010	FT*, RM*, SL*	ST*, SM*	PO*	Wam	Ter.
	10.1	Hoorn <i>et al.</i> , 2010	FT*, RM*, SL*	ST*, SM*	PO*, MF*	NSA	Mar. & Ter.
	9.0 – 10.0	Dobson <i>et al.</i> , 1997; 2001		ST		Atl	Mar.
	9.5 – 8.3	Gorini <i>et al.</i> , 2014	RM, SL	ST	PM	Atl	Mar.
	9.0 – 9.4	Hoorn <i>et al.</i> , 2017	SL	SI	PO	Atl	Mar.
	8.7	van Soelen <i>et al.</i> , 2017	SI (13C, Sm-Nd)	ST		Atl	Mar.
Pliocene	5.3 – 3.6	Latrubesse <i>et al.</i> , 2010		ST, SM	MF	Wam, Sol	Ter.
	3.0	Nogueira <i>et al.</i> , 2013		ST, SM	PO	Sol, Ama	Ter.
Pleistocene	2.5	Campbell <i>et al.</i> , 2001; 2006		ST, SM, SR*	MF	Wam, Sol, Alt*	Ter. Mar.*
	< 1.0	Frailey <i>et al.</i> , 1988		ST		Wam	
	< 0.78	Rossetti <i>et al.</i> , 2015	OL	ST		Sol, Ama	
	0.019	Cremon <i>et al.</i> , 2016	OL SI (14C)	ST		Sol, Ama	
Total		16	11	16	12	16	13

*Reporting/synthesizing data from previous papers.

older than the maximum OSL range are not recordable. In other words, a likely reason for these young OSL ages in Amazonia is that the sediments are slowly being recycled. As a further complication, sediments in most Amazonian sedimentary formations are likely to be of heterogeneous ages, as sediments are buried, exhumed, re-deposited downstream and buried again. For instance, the Içá Formation may include Andean sediments from a megafan that extended far into the Solimões basin (Latrubesse *et al.*, 2010; Wilkinson *et al.*, 2010; Horbe *et al.*, 2013). Such megafans are likely to have formed during pluvial (interglacial) cycles and sea level high-stands, while glacial incision during glacial cycles would have cut deep into floodplains, producing much of the sediment deposition downstream and at modern Amazon Fan (Irion, Kalliola, 2010). Pleistocene dates may therefore record, at least in part, fluvial dynamics during Pleistocene climatic cycles, and do not necessarily contradict a late Miocene age estimate for the onset of a transcontinental river.

A two-stage river capture model. The data reviewed here allow us to recognize at least two stages in the transformation of NSA from a predominately north-draining, to a predominately east-draining, palaeodrainage configuration (Fig. 4). Throughout most of the Late Cretaceous and Paleogene, most rivers in the western portion of NSA drained into the north-trending sub-Andean foreland (orange regions in Figs. 3 and 4), and from there into the proto-Caribbean Sea. These rivers drained basins that today lie to the west of the modern northern Andes (*i.e.* the trans-Andean Magdalena and Maracaibo basins; Aguilera *et al.*, 2013; Pérez-Conseguera *et al.*, 2018), as well as cis-Andean Western Amazon and Solimões basins with headwaters reaching to the Purús and Michicola Arches. Rivers in the eastern portion of NSA drained to the Atlantic Ocean (yellow regions in Figs. 3 and 4). As described above, the Purús Arch has been hypothesized to form part of the western margin of the sub-Andean foreland before the middle Miocene (Courtilot *et al.*, 2003;

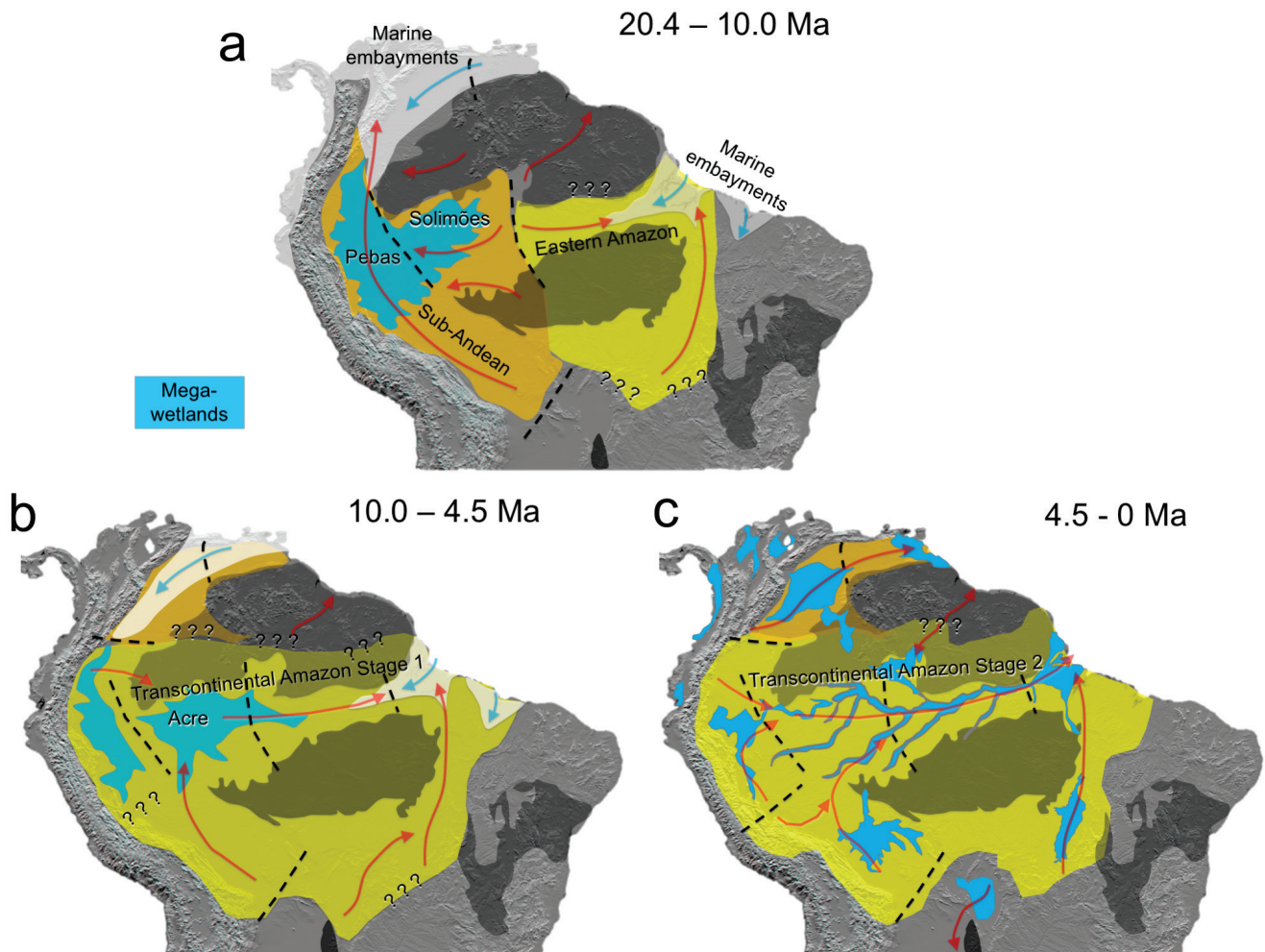


Fig. 4. The changing courses of rivers in northern South America through the Neogene. Reconstructions based on paleogeographic history of major sedimentary basins. **a.** Early and Middle Miocene (20.4–9.0 Ma). North-trending Sub-Andean river basin orange; east-trending Eastern Amazon river basin yellow. **b.** Late Miocene (9.0–5.3 Ma). East-trending transcontinental Amazon river basin (Stage 1). **c.** Middle Pliocene – Recent (c. 4.5–0 Ma). East-trending transcontinental Amazon river (Stage 2).

Caputo *et al.*, 2016; Hurtado *et al.*, 2018). The Eastern Amazon drainage received discharge from some south-trending rivers of the eastern Guiana Shield (*e.g.* proto-Trombetas river) and north-trending rivers of the eastern Brazilian Shield (*e.g.* proto-Tocantins-Araguaia, proto-Tapajos, and proto-Xingu rivers). The watershed boundaries of these northern and southern tributaries of the Eastern Amazon River basin are as-yet poorly delimited, and these boundaries are denoted with question-marks in Fig. 4.

Transcontinental Amazon Stage 1 occurred in the late Miocene (10.0-4.5 Ma), beginning with the first large flux of Andean-derived sediments arriving at the river mouth (van Soelen *et al.*, 2017; Hoorn *et al.*, 2017). Transcontinental Amazon Stage 1 therefore had at least some Andean headwaters, perhaps in the Central Andes at the southwestern margin of the Upper Madeira sedimentary basin, as well as headwaters reaching to the Michicola Arch and Serra da Bodoquena at the southern margin of the Paraguay sedimentary basin (De Alvarenga *et al.*, 2009). The Neogene sedimentary record of the northern Andean basins is largely lacking large coastal deltas, such as the Missoa Formation (early-middle Eocene) of the Maracaibo basin (Aguilera *et al.*, 2013). It is therefore possible that waters of the sub-Andean foreland did not usually flow through a single large river stem, but rather through numerous smaller rivers. The direction of magnitude of water flow from the Western Amazonian basins (*e.g.* Putumayo, Napo, Marañon) during are uncertain during this time, indicated by a dashed arrow in Fig. 4B. Available data indicate the rise of the Vaupes Arch around 10 Ma completely separated the Western Amazon and Llanos basins (Hoorn *et al.*, 2010a, 2010b; Jaramillo *et al.*, 2017). The watershed-divide of the Pebas and Acre mega-wetlands is also uncertain during this time, indicated by question marks in Fig. 4B.

Transcontinental Amazon Stage 2 occurred from about the middle Pliocene to Recent (4.5-0 Ma), with Western Amazonian basins discharging east to the Atlantic, and with Amazonian headwaters extending into the Northern Andes. Before *c.* 4.5 Ma, the Iquitos Arch blocked transport of Andean-derived sediments from the Western Amazon (*i.e.* the North Amazon Foreland Basin or NAFB of Horbe *et al.*, 2013) to the Amazon Fan (van Soelen *et al.*, 2017). This resulted in the accumulation of sediments known as the Nauta/Içá Formation. The greatest increase in total sedimentation rates throughout the basin occurred at the start of the Quaternary, *c.* 2.6 Ma (Figueiredo *et al.*, 2009; Hoorn *et al.*, 2017). Although the Iquitos arch served as a sediment trap during this interval, it did not prevent Andean-derived waters from flowing East through the Solimões and Amazonas sedimentary basins and discharging into the Atlantic. This sediment trap persists in part up the present in the Ucamara depression, serving as the substrate for the Pacaya-Samiria wetlands (Dumont, 1996).

The principal drivers of these changes in transcontinental drainage patterns were: increased Andean denudation and

sediment delivery (Mora *et al.*, 2010; Roddaz *et al.*, 2010), river deflection by basement arches (Hoorn *et al.*, 1995; Costa *et al.*, 2001; Anderson *et al.*, 2016), and mid-continental subsidence possibly driven by subducted slab dynamics (Eakin *et al.*, 2014) and mantle convection (Shephard *et al.*, 2010), and lithospheric responses to sediment loading (Sacek, 2014).

The paleogeographic reconstructions depicted in Fig. 4 have relatively low resolution through time and across space, due to the incomplete nature of currently available data. Uncertainties arise from insufficient stratigraphic age control, conflicting understanding of basin structural configurations, contrasting modes of sediment accommodation, unconformities (attesting to temporal gaps in the sedimentary record), stratigraphic intervals with unclear definitions, and deficient correlations of stratigraphic intervals across basins (Jaramillo *et al.*, 2017).

Watershed migration. Watershed migration occurs due to differential erosion on either side of a catchment divide. In most applications, stream erosive power can be quantitatively described by river discharge and channel slope (Whipple, Tucker, 1999). Despite river discharge being an important parameter controlling the grain size transported by rivers (*e.g.* Lague *et al.*, 2005) which in turn affects stream incision (Sklar, Dietrich, 2004), most of the variance of erosion rates observed globally can be explained by the river channel slope and hillslope gradient, rather than drainage area (*e.g.* Harel *et al.*, 2016). This means that slope usually dominates, such that watersheds are predicted to migrate in the direction of the steeper slope (*e.g.* Gasparini *et al.*, 2007; Whipple *et al.*, 2017). In the Guianas, the prediction is that north-draining Atlantic basins (*e.g.* Essequibo) should capture adjacent Amazon headwaters (*e.g.* Branco). However, the empirical situation seems to be the reverse across this watershed, and others (*e.g.* Casiquiare canal; Stokes *et al.*, 2018). There are also other factors that may affect the direction of watershed migration, including local heterogeneities in sediment/bedrock density, precipitation, subsurface flow, and tectonic uplift. Scale is important in assessing the relative contributions of these factors, which may dominate at different baselines/wavelengths; *e.g.* local (10 km) *vs.* regional (1,000 km).

Changing patterns of connectivity among NSA drainage basins through the Neogene produced several large-scale trends in the direction of watershed migrations, with predictable consequences for biogeography and biodiversity. Each basin-capture was a geodispersal event; *e.g.* the merging of the Solimões and Amazonas basins by breaching of the Purús Arch *c.* 9.4 Ma. Geodispersal events are expected to have enriched the aggregate biota of the expanding Amazon drainage basin by increasing its total area, and also by allowing species to expand their geographic ranges along continuous river channel and floodplain habitat corridors extending between newly connected regions. Each basin capture was also a vicariance event; *e.g.* separation

of the Solimões from the Llanos sedimentary basins across the Vaupes Arch at *c.* 9.4 Ma. Vicariance events are well known to promote speciation by subdividing species ranges across a newly-formed barrier (Nelson, Rosen, 1979; Wiley, 1988). A less-well appreciated consequence of vicariance is that they also promote extinction (Albert, Crampton, 2010; Albert *et al.*, 2017), as populations with a reduced range and population sizes have higher risk of stochastic extirpation (Fagan, 2002).

Here we describe four large-scale trends in watershed migration associated with the formation of the modern Amazon drainage basin.

1. Expansion of Atlantic-draining basins, contributing to the formation of the transcontinental Amazon, at the expense of Caribbean-draining Andean foreland basins (Fig. 5).

2. Expansion of Amazon-draining headwaters at the expense of coastal-draining basins of the Western Guiana Shield (WGS). Evidence of these river captures is readily

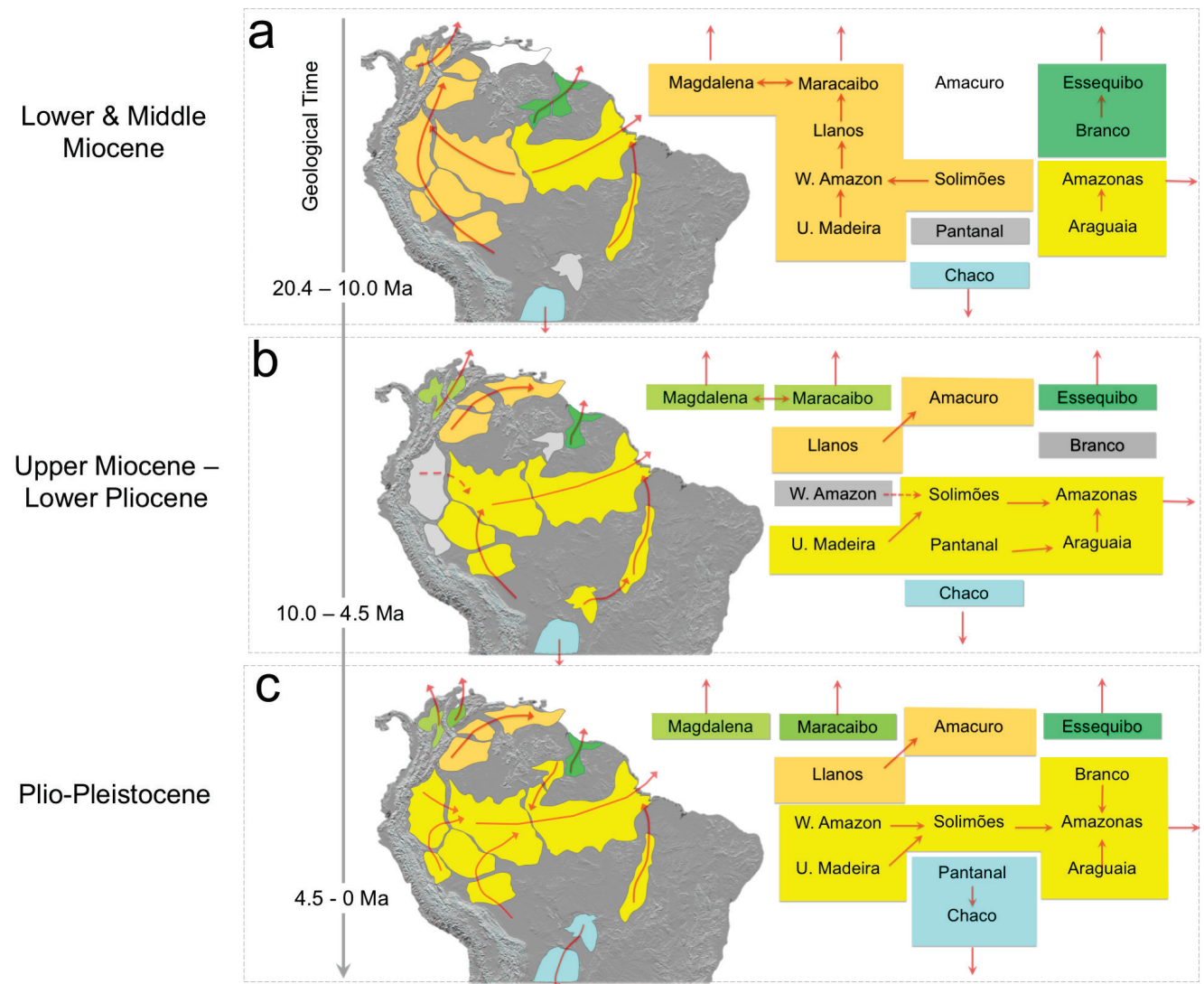


Fig. 5. Summary of hydrological connections among major sedimentary basins of northern South America through the Neogene. Caribbean-draining Andean foreland basins in orange. Atlantic-draining basins contributing to transcontinental Amazon in yellow. Other north Atlantic-draining basins in shades of green. South Atlantic-draining (La Plata) basins in blue. Connectivity as a block-design landscape evolution model at right preserving general spatial relationships. Red arrows depict predominant direction of sediment and water flow. Double-headed arrow indicates bidirectional connections during that time interval. Vicariance events when basins of the same color change to different colors between time intervals; geodispersal events when basins with different colors change to same color. Connections of basins in grey are poorly constrained by available data. Basin in white is entirely marine. “W. Amazon” refers to the combined Putumayo, Napo, Marañón and Ucayali sedimentary basins, “Llanos” to the combined Llanos, and Barinas/Apure basins, “Amazonas” to the combined Amazonas and Marajo basins, and “Essequibo” to the Proto-Berbice basin. Sedimentary basins with four letter abbreviations at left in top panel. Base-maps with modern coastlines and topography to facilitate orientation.

observed in the many signature elbows, U-turns, rapids and waterfalls of the uppermost Negro and Branco basin headwaters (e.g. Casiquiare, Siapa, Mucajá, Uraricoera, Taku-tu; e.g. Goldberg *et al.*, 2017). These landforms indicate a landscape displaced from equilibrium, driven by tectonic event(s) or changes in relative base-levels, all serving to drive river captures (Renwick, 1992; Thorn, Welford, 1994; Kooi, Beaumont, 1996; Church, 2002; Ward *et al.*, 2002; Black *et al.*, 2017; Rodríguez-Tribaldos *et al.*, 2017). These river captures resulted in geodispersal of coastal-basin headwaters to the Amazon, thereby enriching the Amazonian biota, and vicariations isolating sister species on either side of the WGS-Amazon divide.

3. Expansion of Amazon-draining headwaters at the expense of coastal-draining basins on southern (Brazilian) escarpment of the Eastern Guiana Shield (EGS). The river network in the EGS generally approximates a radial pattern, draining away from central uplands of the Tumuc-Humac ridges along the borders of Brazil, French Guiana and Suriname. There are relatively few obvious landforms resulting from river capture of the same magnitude as those depicted in Fig. 4, and much of the drainage network is controlled by tectonic fault lines (de Almeida *et al.*, 2000). However, the rivers of the southern escarpment (e.g. Jarí, Paru, Nhamunda, Trombetas) all flow to the southeast, against the more general landscape gradient that rises towards the east. This lack of conformity between the local direction of river flow and the general tilt of the longer-wavelength topography also indicates a landscape far from erosional equilibrium, with multiple water gaps (*i.e.* putative river captures) across the E-W trending ridge forming the contact between the Paleozoic sediments and the crystalline basement, and extending along the southern EGS margin at about 51.5°-59° W, 1°-2°S.

4. Amazonian headwaters on the Southern Brazilian Shield (SBS) have been lost to encroaching La Plata basins; in particular the Pantanal basin to the Paraguay drainage (Carvalho, Albert, 2011; Assine *et al.*, 2015; Pupim *et al.*, 2015). An interpretation is that the larger Amazon basin gains at the expense of neighbors when erosion dominates the equation for watershed migration, and that basin size is less important than local tectonic forcings near the Andes and especially near the Bolivian Orocline.

Mega-wetlands of Greater Amazonia. Large fluvio-lacustrine and seasonally-flooded wetlands with a similar biotic composition and habitat physiognomy are distributed across much of the modern tropical NSA (Miguez-Macho, Fan, 2012; Fig. 6). Such wetlands, extending over tens to hundreds of thousands of square kilometers, dominate landscapes of the lower Magdalena, Maracaibo, Llanos, Western Amazon (Marañón-Ucayali), middle Negro (Pantanal Septentrionalis), upper Negro (Roraima savanna), and upper Madeira (Llanos de Moxos) basins. In addition, the várzeas of the Amazon River floodplain represents about 2% of the total area of the Amazon drainage basin, or about 12% of all

the Amazon basin wetlands. The modern várzeas, pantanals and seasonally flooded savannahs of NSA all exhibit similar faunal and floristic taxonomic composition (Godoy *et al.*, 1999) and ecosystem phenology (Melack, Hess, 2010).

The large wetlands of modern NSA trace their origins to the geographic and climatic conditions of the Western Amazon during the early Neogene (Hoorn *et al.*, 2010b; Hughes *et al.*, 2013; Antoine *et al.*, 2017; Fig. 7). In the early and middle Miocene, extensive areas of the Western Amazon were covered by mega-wetlands that served as the environment of deposition for the Pebas Formation as it is known in Peru, or the Solimões and Acre Formations as they are known in Brazil. The Pebas/Solimões/Acre Formation consists of fine-grained and cation-rich clay sediments deposited under lacustrine or lacustrine-fluvial conditions (Hoorn, 1993; Räsänen *et al.*, 1995; Gross *et al.*, 2011; Hoorn *et al.*, 2010a; Hovikoski *et al.*, 2010; Wesselingh, Hoorn, 2011). The formation of these early and middle Miocene mega-wetlands was associated with higher eustatic sea-levels of the Miocene climatic optimum (Jaramillo *et al.*, 2017), and the Quechua 1 phase orogeny of Northern Andes (*c.* 17-15 Ma) that depressed the northern Andean foreland basin (Horton, 2017). Lying above these deposits are the Nauta Formation in Peru, or Içá Formation in Brazil. The Nauta/Içá Formation consists of coarse-grained and cation-poor fluvial or deltaic sediments deposited during the Pliocene to Pleistocene (*c.* 4.5-0.1 Ma; Rossetti *et al.*, 2015; Rebata *et al.*, 2006; Wesselingh, Hoorn, 2011; Nogueira *et al.*, 2013).

Mega-wetlands of central and western Amazonia differed in several important regards from the Miocene to the Pliocene. The Pebas/Solimões/Acre Formation is lacustrine-fluvial with a prominence of lacustrine deposits, and the Nauta/Içá Formation is fluvio-lacustrine with a with a prominence of fluvial (*i.e.* riverine) deposits. These differences in depositional environment are associated with a different biotic (*i.e.* taxonomic) composition and habitat physiognomy (Hoorn *et al.*, 2010a; Jaramillo *et al.*, 2010, 2017; Hoorn *et al.*, 2017). As inferred from palynology, the plant species composition of the Plio-Pleistocene Nauta/Içá Formation and modern várzeas differ from that of the Miocene Solimões/Pebas Formation, indicating that characteristic plant composition along the Andes-Amazonian altitudinal gradient, and on the floodplains of the large lowland sediment-rich rivers of modern NSA (e.g. Junk, 1993; Wittmann, Junk, 2003; De Assis, Wittmann, 2011) first appeared in Pliocene (Wesselingh *et al.*, 2001; Wesselingh, Salo, 2006; Hoorn *et al.*, 2010b, 2017; Jaramillo *et al.*, 2017).

Despite these important differences through time and across space, mega-wetland ecosystems have persisted, under different configurations and with differing species compositions, in Western Amazonia for >15 million years, from the early to middle Miocene right up to the present. In other words, for much of the time period since about the middle Miocene (15 Ma), mega-wetlands in one form or another have extended over an immense area of >750,000 km², or about 10% the total surface area of the modern Amazon ba-

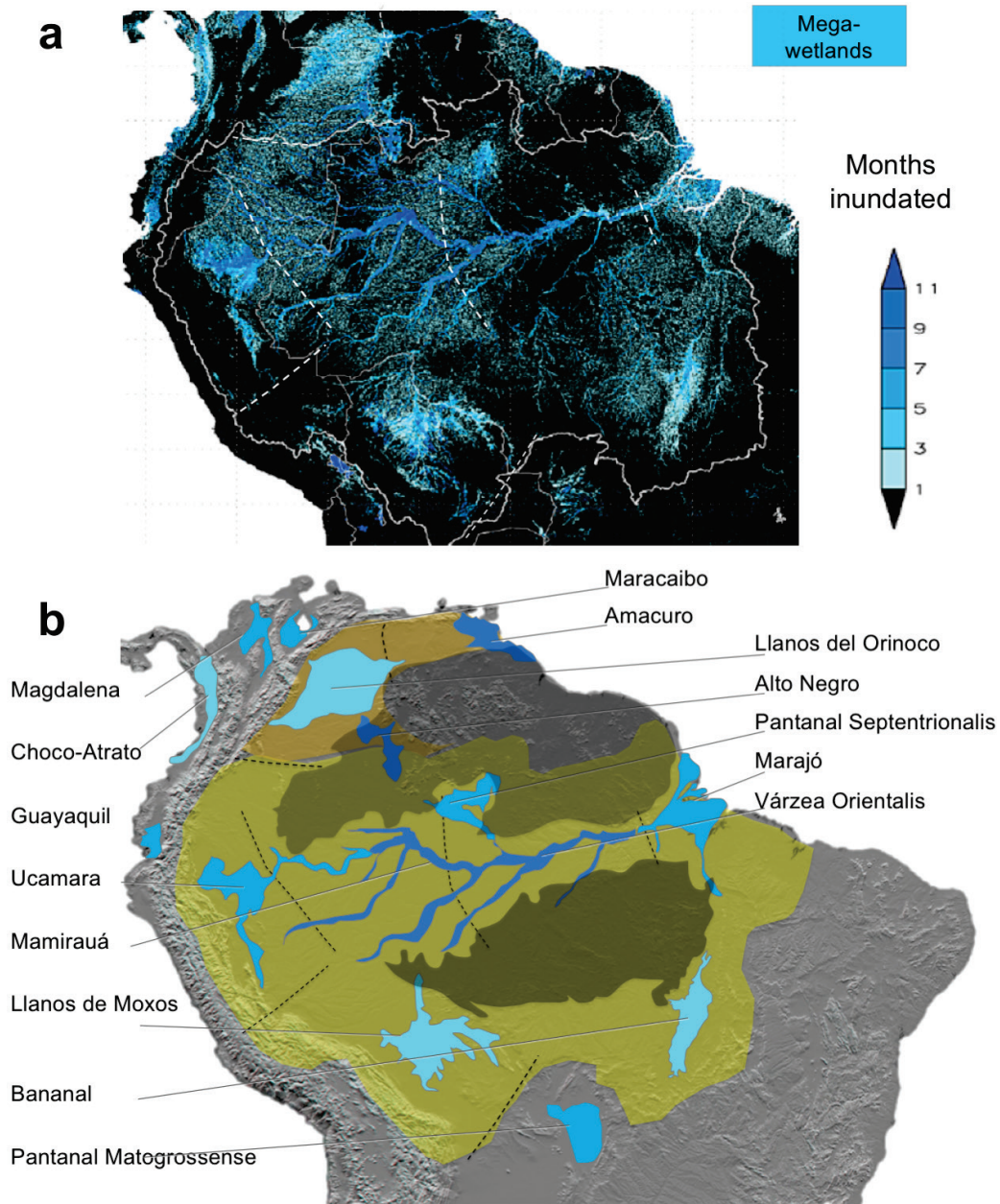


Fig. 6. Mega-wetland systems of modern tropical South America. **a.** Mean number of months of inundation (from Miguez-Macho, Fan, 2012). Simulated flooding frequency as number of months per year over the 10-year period, 2001-2010. **b.** Schematic depiction of 15 largest mega-wetlands (>10,000 km²); intensity of blue shading proportional to average annual duration of inundation. Cartographic conventions as in Fig. 3. Note highly fragmented distribution of mega-wetlands on the modern landscape, and localization of mega-wetlands towards center of larger sedimentary basins.

sin. Understanding the historical continuity of these paleo and modern mega-wetland ecosystems informs historical interpretations of biotic diversification advanced by recent papers, which assume a loss of mega-wetlands from the Miocene to the Recent (e.g. Moreno-Bernal, 2014; Martins *et al.*, 2017; Pérez-Escobar *et al.*, 2017).

Pronounced changes in geographic connectivity of mega-wetlands during this time interval, range from more connected in the late Miocene to more fragmented in the Pliocene to Recent (Fig. 6). Fragmentation of this habitat

contributed to diversification in many freshwater fish taxa, including pimelodid catfishes (Tagliacollo *et al.*, 2015) and apteronotid electric fishes (Evans *et al.*, 2017b). Mega-river captures at the scale of sedimentary basins also allowed taxa originating in the Western Amazon to disperse into the Eastern Amazon, Essequibo, and Parana drainages (Albert *et al.*, 2011a; Dias *et al.*, 2014; Evans *et al.*, 2017a), and isolated taxa in the trans-Andean, Llanos, and Upper Madeira regions (Albert *et al.*, 2006; Albert *et al.*, 2011a; Tagliacollo *et al.*, 2015).

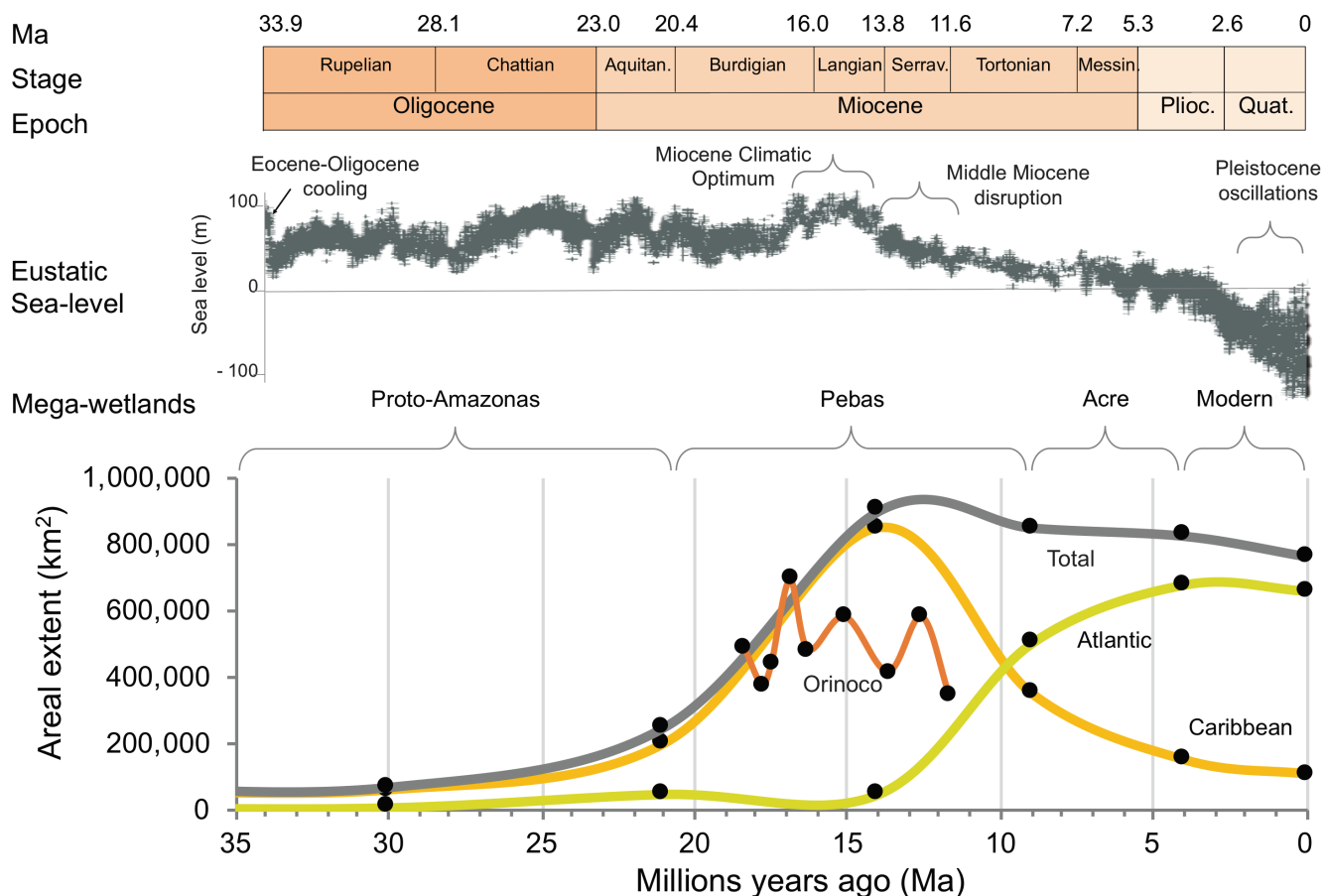


Fig. 7. Growth of mega-wetlands in northern South America. Geological time scale at top. Eustatic sea-level estimates from Zachos *et al.* (2001). Area estimates of for Atlantic and Caribbean draining mega-wetlands from paleogeographic reconstructions in Wesselingh, Hoorn (2010) and Hoorn *et al.* (2017), and for the Orinoco basin by Jaramillo *et al.* (2017). Caribbean-draining Andean foreland basins in orange; Atlantic-draining basins contributing to transcontinental Amazon in yellow. Areas estimated using ImageJ (Abramoff *et al.*, 2004). Curves smoothed using a third-order Bezier Spline.

Conclusions

“Rivers come to be what they are by slow processes of natural development, in which every peculiarity of river-course and valley-form has its appropriate cause (Davis, 1889: 2).”

The evolution of Amazonian drainage basins conformed with changes in the hydrological connections of NSA structural basins through time. These riverscapes evolved under the influences of geological and climatic processes operating over millions to billions of years. These processes include tectonic plate collisions driven by mantle convection resulting in subduction and orogenesis, in combination with lithospheric and surface processes such as fluvial erosion acting under constraints imposed by regional and global climatological regimes (Potter, Hamblin, 2006; Hoorn *et al.*, 2010a, 2017; Galloway *et al.*, 2011).

Modern NSA drainage systems trace their origins to the Cretaceous breakup of Western Gondwana (Potter, 1997; Beard, 2003; Goudie, 2005). Prior to rifting, the predominant flow of drainages in the South American portion of Western

Gondwana was to the west, away from highlands located along the rift zone (Ribeiro *et al.*, 2006; Mapes 2009; Hurtado *et al.*, 2018). Rifting of the South American and African plates about 120-100 Ma changed drainage flows across NSA by the uplift of bounding mountains (*e.g.* Andes to the west, Guiana and Brazilian Shields to the east), and the subsidence of internal basins. Throughout the Upper Cretaceous and Paleogene (*c.* 100-23 Ma) the predominant direction of water flow across NSA was through two catchments; 1) a west-trending Solimões basin and north-trending sub-Andean foreland, together draining to the proto-Caribbean, and 2) an east-trending Amazonas basin draining to the Atlantic (Courtilot *et al.*, 2003; Hurtado *et al.*, 2018). The sub-Andean foreland of the Upper Cretaceous and Paleogene was the geographic location of, and the geological time frame for, the evolutionary origins of major clades of the Neotropical freshwater biota (Lundberg *et al.*, 1998; Albert *et al.*, 2011b; López-Fernández, Albert, 2011).

Oligocene-early Miocene (34-20 Ma) breakup of the Farallon plate into the Nazca and Cocos plates, and the subsequent collision between the Nazca and South American

plates (Barckhausen *et al.*, 2008), uplifted the cordilleras of the Northern Andes, and hydrologically isolated the modern trans-Andean Atrato, Magdalena, and Maracaibo drainages from the cis-Andean Amazon and Orinoco drainages (Albert *et al.*, 2006; Aguilera *et al.*, 2013; Bermúdez *et al.*, 2015). Associated with this orogeny were the exhumation of the Vaupés Arch and sediment overfilling of portions of the sub-Andean foreland, both contributing to the breaching of the Purús Arch and formation of the modern transcontinental Amazon drainage (Horton, 2017). Pleistocene climate fluctuations seem to have had relatively little effect on the formation of regional-scale drainage patterns. Pleistocene shoreline changes may have produced reticulated patterns of connectivity among rivers draining coastal plains, for example along the coastal margins of the Guianas and Brazilian Shields (*e.g.* Thomaz *et al.*, 2017).

Despite the many advances described above in understanding Amazonian geology in the past 20 years, important questions remain unanswered: How big was the sub-Andean drainage basin, and what was the size of the floodplains and river(s) of that basin as compared with those of the modern Amazon basin? Precisely where, when, and in what sequence, did the river captures occur resulting in the modern watersheds of the Araguaia-Paraná, Araguaia-Paraguay, Guaviare-Negro, Branco-Esequibo, Eastern Guianas, and Ucayali-Madeira (indicated with question marks in the paleogeographic reconstructions of Fig. 4)? What if anything was the nature of the hydrological separation between the Pebas and Acre paleobasins in the late Miocene?

The reconstructions of drainage-basin evolution presented here are obviously simplistic and course-grained, in both spatial and temporal dimensions. They are offered to the community as hypotheses to inspire the collection and analysis of new sedimentological and geochronological datasets. The patterns of drainage isolation and merging we propose here may be also compared against results of studies on the historical biogeography of taxa in which evolutionary diversification is thought to be tightly tied to riverscape geography. Future research will require better models and better empirical datasets on which to test those models.

The overall conclusions of this study have quite a different flavor from those of Smith *et al.* (2014), who claimed that landscape evolution is not a decisive factor in Neotropical diversification. It is beyond the scope of this study to link geographic changes in river connections to patterns of diversification in particular taxa. However, the paleogeographic model presented here is consistent with the notion that diversification rates may differ among taxa that exposed to the same landscape evolution events, depending on how lineages persist within, and how easily they may disperse among, geologically persistent sedimentary basins.

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