Chapter 25
Biotic and Landscape Evolution in an Amazonian Contact Zone: Insights from the Herpetofauna of the Tapajós River Basin, Brazil

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Abstract The Amazon basin region, which harbors the largest river system in the world, and which is drained by the Amazon River, has experienced several geomorphological and climatic changes over time. These shifts, as we know, led to distinct signatures in the abiotic variables and the diversification patterns of its native biota. One excellent and yet still understudied model system for biogeographic studies relating biotic diversification to landscape evolution in this region is the Tapajós River basin. Located in an ecotonal zone marked by the presence of geomorphological, climatic and biotic gradients, the basin is crossed by the geographical barrier determined by the Tapajós River, one of the large southern tributaries of the Amazon River. The basin is also marked by high diversity of amphibians and reptiles, with distinct assemblages across its extent and riverbanks. We compare the landscape dynamics within the middle Tapajós River region and the whole basin with a

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comparison of molecular diversification patterns across 16 taxa of amphibians and lizards. For that, we analyze spatial and temporal congruence in diversification through Bayesian gene trees, inter-bank genetic p-distances, and molecular dating based on novel mtDNA data. We find that most groups present spatial diversification patterns concordant with the current position of the Tapajós River, showing high genetic distance between banks. We recovered a continuous range of riverine-associated divergence times, which we group in three main time periods for discussion purposes: (1) ancient divergences, dating from the middle Miocene (ca. 10 Ma); (2) divergences in the late Miocene-Pliocene (ca. 5–3.5 Ma), and (3) more recent divergences, dating to Pleistocene (ca. 2–1 Ma). These results are consistent with a hypothesis of high landscape dynamism in the Tapajós River basin over time, leading to multiple vicariance or colonization events, but cannot be used to discard alternative hypotheses, such as that the river or basin represent areas of secondary contact only. Based on literature and new molecular data, we discuss the evolution of the landscape of the Tapajós River basin and its impact on the diversification of different taxonomic and functional groups.

Keywords Comparative phylogeography · Amazon · Amphibians · Reptiles · Ecotone

1 Landscape Evolution in Amazonia and Its Signatures

There is consensus that the megadiverse Amazon region has been subject to dramatic landscape and biotic changes throughout its history (Leite and Rogers 2013). Since the segregation of the western Gondwana portion and the rising of the South American Plate (Almeida and Hasui 1984), at approximately 140–120 million year ago (Ma; Clark 2018), the region was subject to cycles of erosion and deposition of sediments (Caputo and Soares 2016), uplift and subsidence of terrain (Hoorn et al. 2010a; Latrubesse et al. 2010), mountain orogeny (Horton et al. 2010; Garzione et al. 2017), tectonic adjustments (Rossetti 2014; Caputo and Soares 2016), marine incursions (Jaramillo et al. 2017), climate change (Haffer 1969; Cheng et al. 2013) and vegetational connections to adjacent biomes (Duellman 1979; Silva and Bates 2002; Ledo and Colli 2017). In this historically dynamic region currently lies the largest hydrographic basin of the world, covering much of northern South America and draining through the monumental Amazonas River (Sioli 1968). The emergence and dynamics of this basin over time are intrinsically linked to the spatio-temporal evolution of the South American landscape (Hoorn et al. 2010a; Ribas et al. 2012).

A logical sequence of key events contributed to the formation of the present Amazonian fluvial system (Hoorn et al. 2010b, 2017; Latrubesse et al. 2010). Before the Andean uplift, drainage in the region ran mainly from the Brazilian and Guianan Shields towards the west, flowing into the Pacific Ocean (Hoorn et al. 2010a; Latrubesse et al. 2010). The Andean uplift, with final stages dating from 5–3 Ma,

dammed the western flow of the fluvial system, and, allied to a western depression of the plate, generated a system dominated by lacustrine or swampy environments in the region (the Pebas System; Wesselingh and Salo 2006; Hoorn et al. 2010a, b; Shephard et al. 2010). The subsequent erosion of the Andean mountains led to increasing and intense sediment deposition, which reversed the river system flow eastward, giving birth to the transcontinental Amazonas River (Hoorn et al. 2010b, 2017; Latrubesse et al. 2010; Mora et al. 2010; Shephard et al. 2010; Albert et al. 2018). The river was supplied by the tributaries originated at the recent uplifted Andes and at the ancient terrains of Amazonian Cráton (Hoorn et al. 2010b; Albert et al. 2018).

In addition to geomorphological changes, climatic variation also contributed to the high evolutionary dynamism of the Amazon basin (Cheng et al. 2013; Wang et al. 2017). It cyclically altered the hydrological characteristics of the rivers (e.g. flow, water level, sediment load, and sedimentation rates; Irion et al. 2006), causing marine incursions (Jaramillo et al. 2017), changing the types and extent of habitats present in the interfluves (Haffer 1969; Vanzolini and Williams 1970; Wang et al. 2017; Arruda et al. 2018) and episodically connecting these habitats with adjacent biomes (Batalha-Filho et al. 2012; Ledo and Colli 2017; Arruda et al. 2018). However, scientists still disagree about the precise time scale in which processes such as the establishment of the transcontinental Amazon River (Hoorn et al. 2010b; Latrubesse et al. 2010; Albert et al. 2018), and possible connections between biomes (Batalha-Filho et al. 2012; Ledo and Colli 2017) may have occurred. Such discordance may be caused by the fact that the evolution of the Amazonian landscape and its biota is the result of multiple spatial and temporal processes that triggered different speciation mechanisms (Tuomisto et al. 1995; Tuomisto and Ruokolainen 1997). Multiple sources of evidence are needed to understand these processes and their consequences to the current organization of Amazonian diversity.

Signatures of evolutionary process in the Amazon region may be accessed through currently observed patterns based on two main lines of evidence (Baker et al. 2014; Antonelli et al. 2018): (1) *abiotic*, which investigates, for example, ages and sequences of sediment deposition, location of ancient hydrographic basins, geological breaks, remote sensing, riverine paleochannels, and climatic variation (e.g., Mora et al. 2010; Soares et al. 2010; Rossetti 2014; Rossetti et al. 2014a, b; Latrubesse et al. 2007; Cheng et al. 2013) and (2) *biotic*, investigating the presence and age of fossils, ancient pollens, vegetational dynamics, and levels of intra- and interspecific diversification at distinct biological scales, such as molecular, population and community levels (e.g., Latrubesse et al. 2007; Ferreira et al. 2017; Maia et al. 2017; Soares et al. 2017; Rossetti et al. 2018; Ribas et al. 2018; Ortiz et al. 2018; Godinho and da Silva 2018). Such biotic approach is relevant as the native biota of the Amazon region suffered over time the effects of the intense environmental dynamism, becoming the main players and outcomes of landscape evolution (Antonelli et al. 2009; Baker et al. 2014). Here we integrate abiotic and biotic lines of evidence to understand the evolutionary processes acting in a regional Amazonian set up (the Tapajós River basin). For that, we provide a review of the landscape

history combined with novel molecular data obtained for amphibians and reptiles distributed in this region.

Recognized through sub-disciplines such as "geo-genomics" (Baker et al. 2014) and "trans-disciplinary biogeography" (Antonelli et al. 2018), the integration of different conceptual and methodological approaches based on abiotic and biotic data is becoming more common in studies investigating the evolution of Amazonian landscapes. In many cases, consideration of a single evidence line does not provide substantial advance (Baker et al. 2014), and an integrative framework becomes fundamental to clarify the historical and ecological mechanisms driving current patterns of diversity. For environments with a historical depositional record, such as the Amazonian sedimentary basins (Latrubesse et al. 2005; Hoorn et al. 2010a, b), abiotic information is accessible through sediment layers deposited across time, which act as pages of a book, reporting the sequence of geological and climatic events, even though erosion may periodically erase parts of this sedimentary sequence. Sediment data has led to a substantial accumulation of scientific knowledge regarding the landscape evolution of western Amazon basin, particularly in the Solimões, Madeira, Purus, and Juruá river basins (e.g., Mertes et al. 1996; Latrubesse and Rancy 1998; Latrubesse and Kalicki 2002; Latrubesse and Franzinelli 2005; Latrubesse et al. 2007; Nogueira et al. 2013; Hayakawa and Rossetti 2015; Rossetti et al. 2018). However, in environments with an erosive character, such as the regions of the ancient Brazilian and Guiana Shields (Latrubesse et al. 2005; Hoorn et al. 2010a), the abiotic history is more difficult to reconstruct due to the absence of sedimentological information, making this region a book with several missing pages. This is the case of the eastern Amazonian basins of the Tapajós, Xingu, Tocantins, and Trombetas rivers. In these environments, neotectonic events, mapped through abandoned paleochannels and fault alignments, appear extremely relevant for landscape shaping (Rossetti and Valeriano 2007; Valente and Latrubesse 2012; Leite and Rogers 2013; Rossetti 2014). However, integration with biotic data is fundamental to build a more complete evolutionary history within these regions.

2 The Tapajós River Basin and Its Dual Role as a Barrier for the Biota

The Tapajós River basin is located in northern Brazil, south of the Amazon River (Fig. 25.1), covering portions of the Brazilian states of Pará, Amazonas, and Mato Grosso. This basin has the Juruena, Teles Pires, Jamanxim, and Tapajós rivers as the main tributaries, and its spatial range corresponds to about 10% of the Amazon River basin (Sioli 1968), being the fifth largest tributary sub-basin of the Amazonas River, and supplying about 6% of the water in this river (Latrubesse et al. 2005).
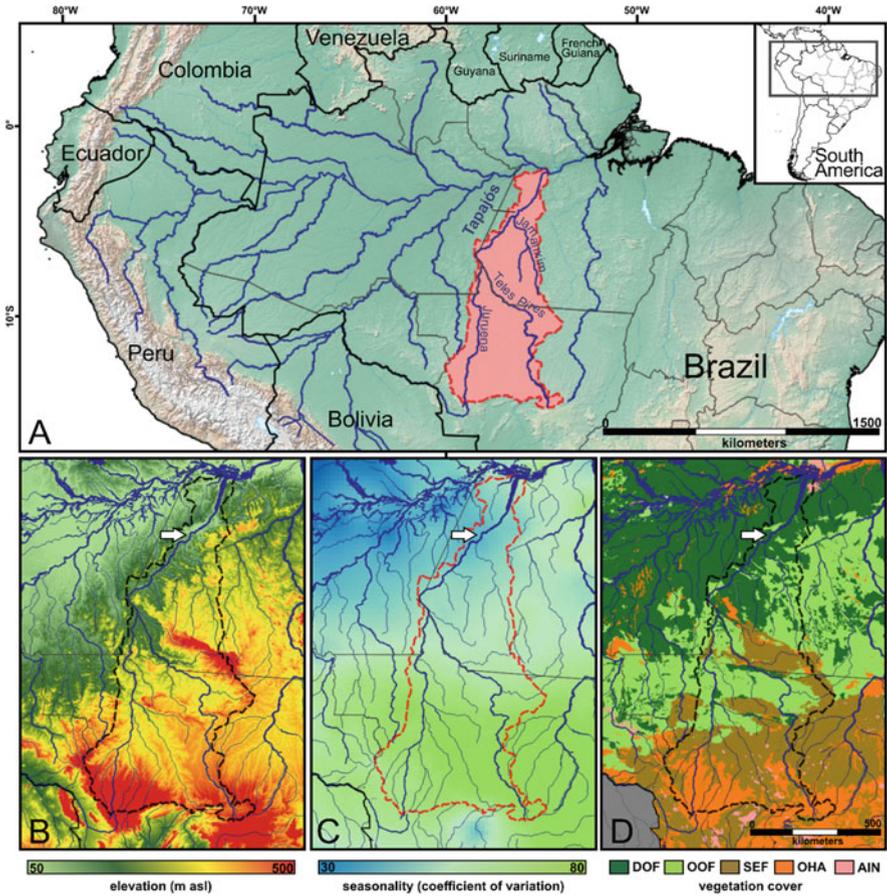
Fig. 25.1 Location of the Tapajós River basin (dashed lines) in relation to the Northern South America and the Amazon basin (**a**) and upon elevation (**b**), seasonality (**c**) and vegetation (**d**) backgrounds, showing the ecotonal character in which the basin is located based on geomorphological, climatic and vegetational variation, in both North-South and west-east directions. The white arrow represents the zone of geological transition between the Brazilian Shield and Amazonas sedimentary basin. Vegetation cover: (DOF) Dense Ombrophylous Forest; (OOF) Open Ombrophylous Forest; (SEF) Seasonal forests; (OHA) Open habitats; (AIN) Anthropic influence

Geologically, the Tapajós River basin runs through two main compartments: its upper and middle courses are located in the Brazilian Shield, lying on ancient Pre-Cambrian (>541 Ma) rocks (Santos et al. 1975), presenting 2–3 km of horizontal extension between the banks, and draining with a predominantly erosive character. Its lower course, in contrast, is located in the more recent Cenozoic (66 Ma to present) sedimentary basin of the Amazon River, extending to ca. 10–20 km of extension between the banks, and favoring the depositional character and the formation of alluvial plains (Santos et al. 1975; Araujo et al. 1976; Silva et al.

1980). These two geological compartments are segregated by a short region of Paleozoic sediments (455–300 Ma) in their contact zone, resulting from the historical sedimentation process of the Brazilian Shield (Santos et al. 1975). Due to this origin and geomorphological setting, the current spatial conformation of this basin is asymmetric, especially in its upper and middle course, where the main trunk river runs through the border of the Brazilian Shield (in contact with the Solimões sedimentary basin), and its main tributaries drain from the east (Santos et al. 1975; Araujo et al. 1976; Silva et al. 1980). This conformation generates a scenario in which the larger tributaries in the left bank of the Tapajós River are influenced by the Solimões sedimentary basin, while the larger tributaries on the right bank drain older terrain in the Brazilian Shield (Santos et al. 1975; Araujo et al. 1976; Silva et al. 1980; Moraes et al. 2016). Because of this erosive character over shield rock, with low sediment input, the rivers of this basin transport little amounts of dissolved sediments (Latrubesse et al. 2005), leading to their classification as "clear-water" rivers, in contrast to other Amazonian "black water" (with low amount of sediments and high amount of organic material dissolved in the water column) and "white water" rivers (with high amount of sediments dissolved in the water column; Sioli 1968; Junk et al. 2011).

This geological difference between the upper/middle and lower courses of the Tapajós River basin is also evident in other aspects of the current landscape (Santos et al. 1975; Araujo et al. 1976; Silva et al. 1980). The upstream courses, which run embedded in the rocky bed of the Brazilian Shield, present numerous rocky outcrops in the river channels, especially evident in the annual dry period (Fig. 25.2d). For this reason, the water flow in these courses is more intense, and rocky rapids, unevenness, and waterfalls are common, becoming especially abrupt in the contact zone between the main geological compartments, near the village of São Luis do Tapajós (Fig. 25.1). Given this hydromorphology, these courses of the Tapajós River basin are frequent targets of projects for generation of hydroelectric energy (Latrubesse et al. 2017). As the course of the Tapajós River reaches its lower portion, rocky outcrops and rapids become scarce and the river acquires a slower water flow, becoming a huge lentic "ria-lake", draining to the channel of the Amazon River (Irion et al. 2006) (Fig. 25.1).

Climatically, the Tapajós River basin presents a mean annual temperature range from 21 °C to 27 °C (Alvares et al. 2013). Its precipitation regime is intermediate relative to the two distinct dynamics observed in western vs. eastern Amazonia (Sombroek 2001; Cheng et al. 2013) (Fig. 25.1b). The climatic pattern of western Amazonia is characterized by a low annual seasonality and high annual rainfall, which gradually changes towards Southern and eastern Amazonia, increasing in annual seasonality and decreasing in annual rainfall (Alvares et al. 2013) (Fig. 25.1b). It has been inferred that these two climatic regimes had distinct histories throughout the Quaternary, modifying the structure and affecting the stability of the forests in these regions (Cheng et al. 2013; Wang et al. 2017), and enabling periodical connections with other Neotropical rainforests (Cheng et al. 2013; Ledo and Colli 2017). Such dramatic cyclical changes in climatic patterns would have
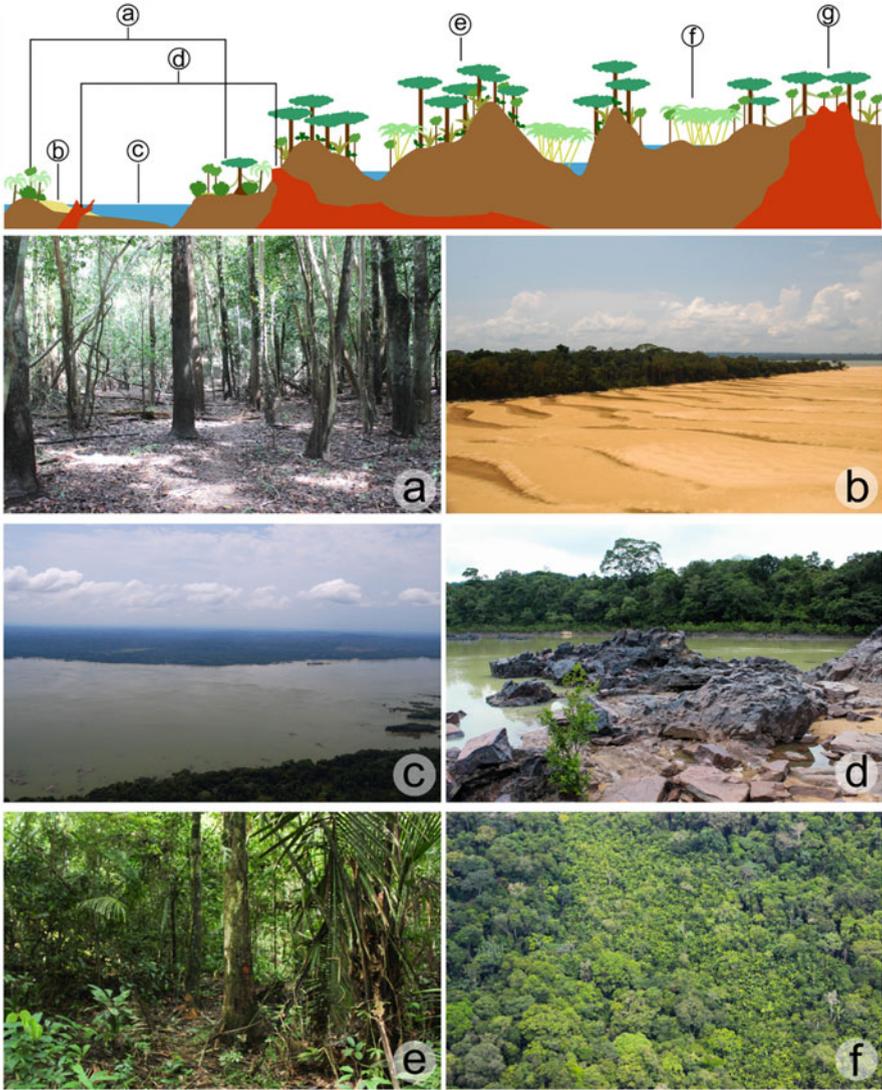
Fig. 25.2 Generalized vertical profile and photographs of middle Tapajós River region, evidencing changes in landscape, terrain and vegetation structure. (**a**) Periodically flooded forest (*igapó*) from fluvial islands and banks of large rivers; (**b**) sand deposit (beach); (**c**) main course of the Tapajós River near the municipality of Itaituba, Pará state; (**d**) rocky outcrops of the crystalline basement; (**e**) non-flooded Dense Ombrophilous Forest; (**f**) alluvial Dense Ombrophilous Forest from banks of small streams evident in lighter green, varying in degrees of palm predominance; (**g**) non-flooded Open Ombrophilous Forest. Photographs by Dante Pavan (**a**, **d**, **f**), Elizângela Brito (**b**, **c**) and Leandro Moraes (**e**)

affected and altered the biota native of these climatic regions (Cheng et al. 2013; Wang et al. 2017).

Patterns of climatic and geological variation can also be observed in the current forest cover associated with the Tapajós River. On the left bank there is a predominance of Dense Ombrophylous Forest (Fig. 25.2e), an exuberant and diverse forest type, with complex stratification, massive presence of lianas and epiphytes, and high capacity of local climate regulation (Terezo et al. 1975; Coêlho et al. 1976; Loureiro et al. 1980), influenced by the more humid and less seasonal climate from the western Amazonian sedimentary basin. On the right bank of Tapajós River the Open Ombrophylous Forest dominates, a less-stratified forest type with lower canopy, greater presence of clearings, and more dense understory (Terezo et al. 1975; Coêlho et al. 1976; Loureiro et al. 1980), influenced by the drier and seasonal climate from eastern Amazonia (Brazilian Shield), and the contact between the Amazon-Cerrado biomes (Fig. 25.1d).

Based on these current patterns, it is evident that the Tapajós River basin, especially its upper and middle courses, is located in a climatic, geomorphological, and vegetational transition zone (Fig. 25.1). We propose that this ecotonal character be taken into account when investigating the spatial and temporal patterns of diversification of its associated biota (Moraes et al. 2016). Ecotonal regions are known to possess both unique and mixed ecological characteristics between adjacent environments (Smith et al. 1997; Werneck et al. 2012a). In Amazonia, forest ecotones present less obvious transitions (Cohn-Haft et al. 2007; Ortiz et al. 2018) when compared to closed-open environment contacts such as that between the Amazon and the Cerrado (Ackerly et al. 1989). Because the Tapajós River course crosses this ecotonal zone, acting as a physical barrier upon an environmental gradient (Moraes et al. 2016), its basin is a good model for studies of biotic responses to landscape evolution.

3   The Tapajós River Basin's Dynamic History

Unlike rivers running through sedimentary basins, where recent geomorphological dynamism is primarily driven by sedimentation patterns (Gascon et al. 2000), rivers running in the ancient terrain of the Brazilian Shield suffer mainly the effects of recent conformational changes associated with neotectonic events, generating course captures and recaptures (Rossetti and Valeriano 2007; Dagosta and de Pinna 2017). Geological maps show a high density of fractures and volcanic intrusions in the cratonic region of the Tapajós River basin, some with recent signs of reactivation (Santos et al. 1975). In addition to the geomorphological change that may have affected the conformation of the rivers inside the Tapajós River basin, recent climatic change likely modified the extent of available terrestrial ecosystems and the water level of the large rivers (Irion et al. 2006; Cheng et al. 2013; Wang et al. 2017), potentially promoting multiple periods of contact and allopatry between populations. Patterns of Amazonian fish diversity inside cratonic river basins also suggest a

dynamism of river channels (Dagosta and de Pinna 2017), with the Tapajós River basin an example of a mixed assemblage where communities in the tributaries Jamanxim, Juruena and Teles Pires are more similar to other Brazilian Shield rivers, and those in the main course of the Tapajós River are more similar to rivers from the Guiana Shield and the sedimentary basin of Amazonas River (Dagosta and de Pinna 2017).

Brazilian Shield rivers have been associated with recent diversification events when compared to rivers that run in other geological formations, such as the Negro, Madeira and lower Amazonas (Ribas et al. 2012; Silva et al. 2019). This recent diversification was indirectly evident when all interfluves segregated by Xingu and Tocantins rivers were considered a single unit in former delimitations of Amazonian areas of endemism, mainly due to the fact that endemism was then mapped based on phenotypically-informed taxonomy only (Cracraft 1985). It was only after refined analyses of biotic diversity that the areas of endemism segregated by the Xingu and Tocantins rivers were recognized (da Silva et al. 2002). With the advent of molecular techniques, these three distinct areas of endemism delimited by Xingu and Tocantins rivers were also recovered, with most recent splits between taxa mostly associated with these rivers from the Brazilian Shield (Ribas et al. 2012; Silva et al. 2019).

These observations of shallow divergences across Brazilian Shield rivers appear counterintuitive, as those rivers run through older terrains—but this pattern seems recurrent as the volume of available data and analytical capacity increase (Silva et al. 2019). With longer time since their origins, rivers of the Brazilian Shield would have had an equally greater probability of experiencing course changes promoted by geomorphological and climatic dynamism over time (Irion et al. 2006; Wang et al. 2017), making them more permeable—or this region unsuitable for several Amazonian taxa until a recent period (Silva et al. 2019). These recent landscape disturbances or regional extinctions followed by reoccupation would have promoted equally recent splits between biological populations from Brazilian Shield (Silva et al. 2019).

Based on abiotic and biotic evidence for this region, one landscape evolution hypothesis for the Tapajós River basin includes the discharge of the ancient rivers (the proto-Teles Pires, proto-Juruena and proto-Jamanxim rivers) towards the lower Amazonian regions when the basin was craton-oriented (Hoorn et al. 2010a), or even more recently. This is consistent with the finding of Pleistocenic sediments from the Tapajós River basin near the region of Manaus (Caputo and Soares 2016; Fig. 25.3). During that craton-oriented Amazonian period, possible connections between sub-basins within the Brazilian Shield (caused by river captures due to neotectonic events) may have increased the similarity of the aquatic biota of these three proto-rivers (Dagosta and de Pinna 2017). Tectonic and geomorphological rearrangements derived from the positive inversion of the Cachimbo Graben between the proto-Teles Pires and the proto-Juruena rivers, in relation to the proto-Jamanxim River, resulted in a positive structural arch which divided the Amazonas and Solimões basins (Wanderley-Filho et al. 2010) (Fig. 25.3). This event, followed by the Andean uplift, the subsidence of the sub-Andean region, and the formation of the transcontinental Amazon River (Hoorn et al. 2010a; Caputo and Soares 2016), would have modified
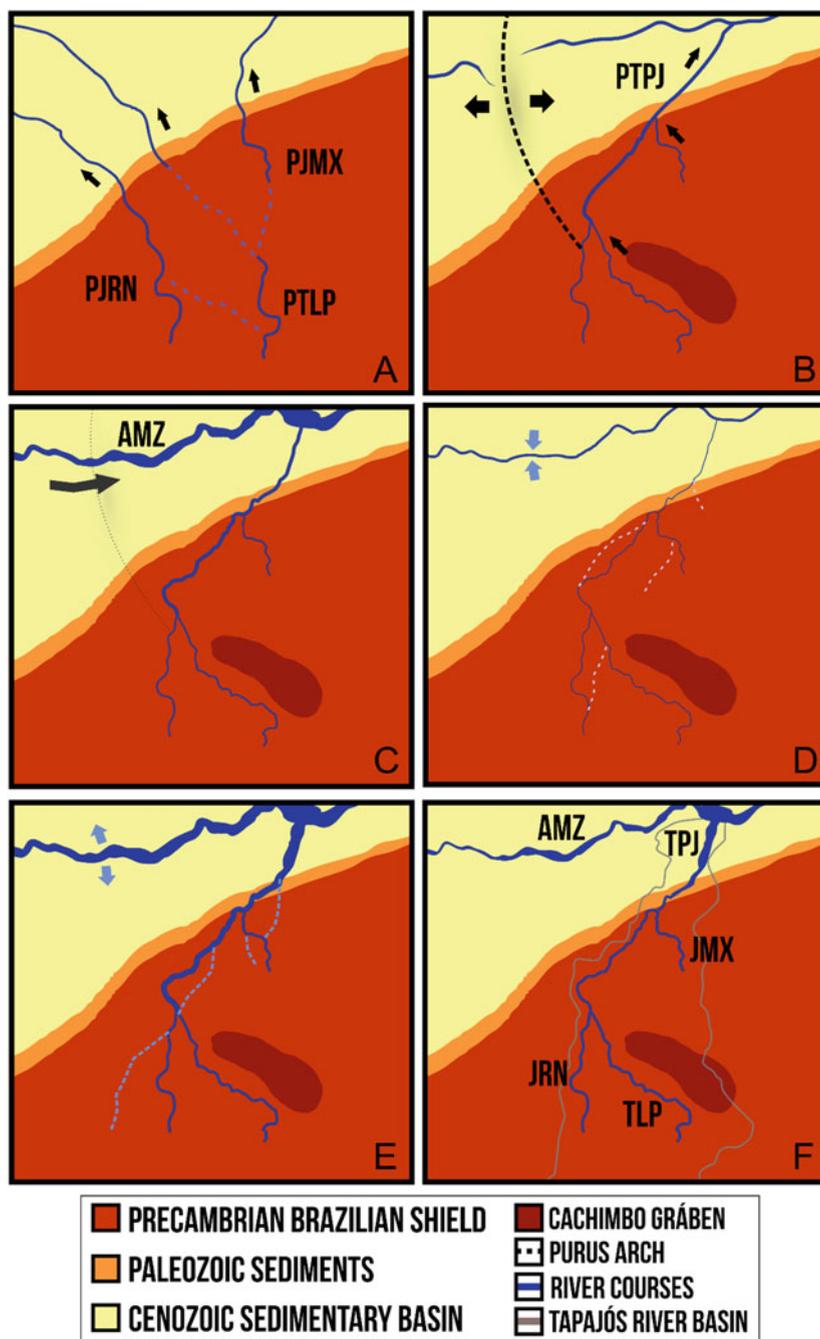
Fig. 25.3 Schematic hypothetic representation of the main spatial and temporal sequence of events hypothesized to have modified the Tapajós River basin landscape, consequently affecting its native biota. Accurate timing of such events remains unknown (see text for additional details and references). (**a**) Ancient discharge of Brazilian Shield rivers proto-Teles Pires (PTLP), proto-

the conformation and joined the proto-Teles Pires and proto-Juruena rivers. This connection of two large rivers would have discharged a large volume of water in a new channel that bypassed westward the Cachimbo Graben area, adjusted to a large fracture line (Tapajós line), and formed the current Tapajós River course (Fig. 25.3). This course also captured the proto-Jamanxim River and all smaller tributaries of its right bank that ran through the Brazilian Shield. Although this chronological sequence is plausible based on the evolution of the cratonic and sedimentary landscape of the Amazon basin (Hoorn et al. 2010a; Caputo and Soares 2016), the time periods in which these events would have occurred remain unknown (Fig. 25.3).

During the Pleistocene, the landscape in the basin would have been modified mainly by changes in the water level of the Tapajós River and its tributaries, due to glacial climatic variations, affecting river discharge and base level (Irion et al. 2006, 2010). The high sea level in interglacial periods may have led to an increase in the river base level within the Tapajós system, consequently increasing the barrier effect of the rivers to the surrounding biota and damming the lotic ria-lake system in its low course, as currently observed (Irion et al. 2006) (Fig. 25.3).

4   Amphibians and Reptiles of the Tapajós River Basin

The geographic distribution of the amphibians and reptiles of the Tapajós River basin appears to be strongly influenced by the marked environmental and historical heterogeneity described above. Although many generalist taxa are widely distributed across the basin (Duellman 1979), some are restricted to or are more abundant in distinct zones, causing striking shifts in beta diversity, especially between the

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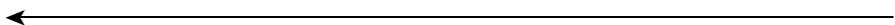
Fig. 25.3 (continued) Juruena (PJRN) and proto-Jamanxim (PJMX) in sedimentary basin, when the Amazon basin was craton-oriented, with the possible occurrence of riverine courses connections; (**b**) uplift of the Cachimbo Gráben resulting in geomorphological adjustments creating a central Amazonian watershed. These events may have connected the courses of proto-rivers Teles Pires and Juruena, discharging a large volume of water in the system, creating the proto-Tapajós River (PTPJ) embedded in geological faults, and connecting it to the proto-Jamanxim River. At this period, the discharge of Tapajós River basin was fully directed to the Amazonas sedimentary basin and eastern Amazonia; (**c**) The events arising from the Andean uplift and tectonic adjustments connected the western and eastern Amazonian sedimentary basins, generating the huge transcontinental Amazonas River. The Tapajós River basin becomes tributary to this system, (**d**, **e**) Intense climatic variations modified the sea level and favored periods of marine incursions and retractions, damming the ria-lake in the lower Tapajós River during higher sea-levels events. Such variation modified the amount of water discharging in the Tapajós River cratonic basin over time and its permeability to the native biota. The permeability is also affected by events of riverine course changes by neotectonic adjustments (dashed lines); (**f**) current conformation of the Tapajós River basin and its boundaries, with the main tributaries Teles Pires (TLP), Juruena (JRN), Jamanxim (JMX) and Tapajós (TPJ) rivers. For further details involving the current spatial variation of the landscape within this basin see Fig. 25.1

Brazilian Shield and the sedimentary basin. For example, the amphibian taxa *Boana punctata*, *B. raniceps*, *B. lanciformis*, *Lysapsus bolivianus*, *Scinax nebulosus*, *Rhinella* gr. *granulosa*, *Sphaenorhynchus* spp. *Scarthyla goinorum*, *Trachycephalus typhonius*, *Dendropsophus walfordi*, and the reptile taxa *Varzea bistriata*, *Anolis auratus*, *Gymnophthalmus* sp., *Crocodilurus amazonicus*, *Dracaena guianensis*, *Chironius carinatus* and *Crotalus durissus* are more abundant or only occur in the lower portion of the Tapajós River basin (sedimentary basin, Fig. 25.1a; Ribeiro-Júnior 2015a, b; Ribeiro Júnior and Amaral 2016, 2017; Frost 2019; Uetz et al. 2019), where the terrain is flatter and presents a well-developed alluvial plain, altering the flooded forest type and increasing its fertility, favoring the presence of aquatic macrophytes and the occurrence of water pools in the banks of large rivers (Sioli 1984; Piedade et al. 2010). Those taxa depend on these habitat characteristics throughout their life cycles. On the other hand, in the middle and upper portions of the basin, inserted in the Brazilian Shield (Fig. 25.1a), the more rugged terrain, with greater drainage capacity, lower development of alluvial plains, and flooded forests with lower fertility (Sioli 1984; Piedade et al. 2010), favors the occupation by other taxa, such as the amphibians *Adelphobates galactonotus*, *A. castaneoticus*, *Allobates crombiei*, *A. magnussoni*, *Ameerega munduruku*, *Proceratophrys concavitympanum*, and the reptiles *Gonatodes tapajonicus* and *Rondonops biscutatus* (Lima et al. 2014; Ribeiro-Júnior 2015a, b; Ribeiro Júnior and Amaral 2016, 2017; Frost 2019; Uetz et al. 2019). Other examples are detailed below, as the target region of this study is located on the northern edge of the Brazilian Shield terrain. The southern limits of the geographic distribution of many of these taxa typical from the Brazilian Shield are virtually unknown, being the environmental variation present in the Serra do Cachimbo and the transition with the Cerrado biome the most plausible determinants of their distribution boundaries (Fig. 25.1c). These environments at the upper portion of Tapajós River basin are then occupied by other unique taxa, typical from open habitats, such as the amphibians *Dendropsophus cachimbo*, *Adenomera martinezi*, *Scinax villasboasi*, and the reptiles *Hoplocercus spinosus*, *Tropidurus insulanus*, *Tupinambis matipu*, *Cercosaura eigenmanni*, *C. olivacea*, *Chironius flavolineatus* and *Lygophis meridionalis* (França et al. 2006; Ribeiro-Júnior 2015a, b; Ribeiro Júnior and Amaral 2016, 2017; Silva et al. 2018; Sturaro et al. 2018; Frost 2019; Uetz et al. 2019).

Focusing on the amphibian and reptile assemblages of the middle course of the Tapajós River, intensive standardized sampling in 11 localities from both banks of the river recorded a high diversity of species (193 taxa, Moraes et al. 2016) and challenged previously recognized biogeographic patterns (Jenkins et al. 2013; Moraes and Pavan 2017, 2018; Moraes et al. 2014, 2016, 2017a, 2019a, b). Since 2012, 10 amphibian and 3 reptile taxa recorded by Moraes et al. (2016) were formally described as new species (6% from total), 13 amphibian and 22 reptile taxa had their taxonomic status revised (18% from total), and about 30 amphibian and 9 reptile taxa still represent undescribed taxonomic entities (20% from total). Such expressive results highlight the importance and necessity of intensive faunal inventories, integrative data processing, and taxonomic refinement of databases to fill knowledge gaps in this Amazonian region and achieve greater accuracy in

biogeographic analyses (Moraes et al. 2017b). High taxonomic diversity was also detected in this region for other vertebrate groups, such as mammals and birds (Oliveira et al. 2016; Maximiano et al. 2017).

Previous analyses of assemblage structure in the Tapajós river basin suggest that a dynamic equilibrium between regional historical events (i.e., riverine barriers) and local ecological conditions (i.e., flooding gradients) may have contributed (and still contribute) to the origin and maintenance of current species' geographic distribution patterns (Moraes et al. 2016). Specifically, they demonstrated changes in species composition along the flooding gradient, and differential effects of large rivers as barriers to dispersal in distinct zones of the flooding gradient (Moraes et al. 2016). Integration of biogeographic and ecological information shows that the permeability of a geographic barrier to Amazonian amphibians and reptiles unequally affects different taxonomic, functional and ecological groups, a result similarly found in other vertebrates (Gascon et al. 1998, 2000; Burney and Brumfield 2009; Fouquet et al. 2015; Naka and Brumfield 2018). The ecotonal zone crossed by the Tapajós River was also identified as a potential driver of geographic distribution patterns of amphibian and reptile assemblages on both banks of the middle Tapajós River (Moraes et al. 2016).

Building on the biogeographic patterns previously reported for this ecotonal landscape, and given the cratonic location of the basin (which is expected to result in a less dynamic geomorphological evolution), *we here implement a multi-taxa molecular study of amphibians and reptiles belonging to different functional groups, to (1) expand our knowledge about regional patterns of diversification and (2) to test the potential effect of the middle Tapajós River as a geographic barrier across space and time*. For that, we sequenced regions of the mitochondrial (mtDNA) genes *16S*, *ND4* and *COI* for 180 individuals representing taxa with distinct body sizes and ecological affinities, through methods described in the online Supplementary Material of this chapter. Comparative molecular data have become increasingly relevant to integrative studies of community assembly and evolutionary history by detecting shared spatial and temporal diversification patterns (Turchetto-Zolet et al. 2013; Baker et al. 2014), which are essential to identify the processes that generate and maintain current diversity patterns and landscape evolution (Bermingham and Moritz 1998). By investigating diversification of multiple co-distributed taxa, and evaluating spatial-temporal co-divergences, one can validate biogeographic models or hypotheses such as the relative effect of a river as a primary promoter or secondary contributor to diversification (Smith et al. 2014). To shed light on this issue, we compare the diversification patterns shown by 11 amphibian and five lizard taxa from the middle Tapajós River.

We focus on amphibians and reptiles because they are increasingly relevant model organisms in integrative studies of the Amazonian biota and landscape evolution (Marshall et al. 2018), given their sensitivity to climatic and environmental changes (Winter et al. 2016; Diele-Viegas et al. 2018) and relatively low individual mobility (Simões et al. 2014; Marshall et al. 2018). For the purposes of this study, we selected taxa present in high local abundances, and based on their distinct body sizes and ecological preferences, which may influence dispersal ability and hence genetic

structure and diversification rates (Burney and Brumfield 2009; Cadena et al. 2011; Smith et al. 2014; Fouquet et al. 2015; Moraes et al. 2016; Harvey et al. 2017; Table 25.1, Figs. 25.4 and 25.5).

5 Amphibian and Reptile Diversification Across Space and Time

We used Bayesian phylogenetic gene trees to describe the spatial structure of infra-specific lineages in relation to the Tapajós River (see details in Supplementary Material in online version of this chapter). Haplotype sharing across river banks was observed in 31% of the analyzed taxa (5/16; the amphibians *B. tapajonica*, *L.* aff. *knudseni*, *O. taurinus* and *R.* gr. *margaritifera*, and the lizard *P. plica*), indicating the flow of individuals and genes between banks, or incomplete lineage sorting (Fig. 25.6). The remaining 69% taxa (11/16; the amphibians *A. andreae*, *A.* gr. *heyeri*, *A.* gr. *masniger*, *B. cinerascens*, *B.* gr. *albopunctata*, *P.* gr. *conspicillatus* and *R. magnussoni*, and the lizards *A. angulatus*, *A. reticulata*, *C.* gr. *ocellata* and *C. amazonicus*) have reciprocally monophyletic lineages on opposite banks of the Tapajós River (Figs. 25.6 and 25.7).

The lineages of *Adenomera andreae* present low values of genetic distance between opposite margins, suggesting relatively recent divergence (Fig. 25.7). In five amphibian taxa (*B. cinerascens*, *B.* gr. *albopunctata*, *A.* gr. *heyeri*, *A.* gr. *masniger*, *P.* gr. *conspicillatus*), the average genetic distance between banks varied from 4% to 11%, surpassing the threshold recognized for interspecific divergence (Fouquet et al. 2007a, b; Kok et al. 2018; Fig. 25.7). This suggests cryptic diversity, a common finding in Amazonian amphibians (Fouquet et al. 2007b; Vacher et al. 2017). Within those taxa, only five distinct lineages are formally described: *Boana leucocheila* and *Boana multifasciata* (from *B.* gr. *albopunctata*), *Allobates masniger* and *Allobates nunciatus* Moraes et al. 2019b (from *A.* gr. *masniger*), and *Pristimantis latro* (from *P. gr. conspicillatus*), while several other lineages remain unnamed, although they present clear phenotypic divergences in morphology and advertisement calls and are presently under description (authors, pers. obs.). Within the lizards, genetic distances between margins were also high; in three taxa (*A. reticulata*, *A. angulatus* and *C. amazonicus*) they surpass the proposed threshold of interspecific divergence based on the *ND4* gene (Kok et al. 2018; Fig. 25.7), ranging from 12% to 28% in average. This observation is consistent with the high levels of molecular differentiation associated with overall phenotypic conservatism reported for other lizard species in Amazonia (Geurgas and Rodrigues 2010; Nunes et al. 2012; Sturaro et al. 2018). Further analyses may revise the taxonomic status of these cryptic lizard lineages.

We did not detect high prevalence of riverine-related structure associated with any particular trait category regarding body size, forest type, or microhabitat use. Reciprocal monophyly across river banks was detected in taxa with small (e.g., *A.*

Table 25.1 Focal amphibian and lizard taxa from banks of Tapajós River, Pará State, Brazil, from which we investigated spatial and temporal diversification patterns with a molecular approach

Class	Order	Family	Taxa	Body size (mm)	Forest type	Microhabitat	N
Amphibia	Anura	Aromobatidae	*Allobates* gr. *masniger*	20	Non-flooded	Terrestrial	27
Amphibia	Anura	Craugastoridae	*Pristimantis* gr. *conspicillatus*	40	Non-flooded	Terrestrial	58
Amphibia	Anura	Leptodactylidae	*Adenomera andreae* (Müller, 1923)	20	Non-flooded	Terrestrial	22
Amphibia	Anura	Leptodactylidae	*Adenomera* gr. *heyeri*	25	Non-flooded	Terrestrial	11
Amphibia	Anura	Leptodactylidae	*Leptodactylus* aff. *knudseni*	140	Non-flooded	Terrestrial	8
Amphibia	Anura	Hylidae	*Boana cinerascens* (Spix, 1824)	35	Flooded	Arboreal	4
Amphibia	Anura	Hylidae	*Boana* gr. *albopunctata*	65	Flooded	Arboreal	7
Amphibia	Anura	Hylidae	*Osteocephalus taurinus* Steindachner, 1862	90	Generalist	Arboreal	13
Amphibia	Anura	Bufonidae	*Rhinella* gr. *margaritifera*	70	Non-flooded	Terrestrial	23
Amphibia	Anura	Bufonidae	*Rhinella magnussoni* Lima et al. 2007	45	Non-flooded	Terrestrial	16
Amphibia	Caudata	Plethodontidae	*Bolitoglossa tapajonica* Brcko et al. 2013	45	Non-flooded	Arboreal	5
Reptilia	Squamata	Gymnophthalmidae	*Arthrosaura reticulata* (O'Shaughnessy, 1881)	55	Non-flooded	Terrestrial	8
Reptilia	Squamata	Gymnophthalmidae	*Cercosaura* gr. *ocellata*	50	Non-flooded	Terrestrial	9
Reptilia	Squamata	Gymnophthalmidae	*Alopoglossus angulatus* (Linnaeus, 1758)	55	Non-flooded	Terrestrial	4
Reptilia	Squamata	Sphaerodactylidae	*Chatogekko amazonicus* (Andersson, 1918)	20	Non-flooded	Terrestrial	15
Reptilia	Squamata	Tropiduridae	*Plica plica* (Linnaeus, 1758)	145	Generalist	Arboreal	8

Body size (mean of snout-vent length based on field data), ecological preferences (typical forest types and microhabitats in which they are present), and number of specimens included in analyses (N), are detailed

Fig. 25.4 Focal amphibian taxa from the banks of the Tapajós River and studied here (**a**) *Allobates masniger* (Morales, 2002) (from *Allobates* gr. *masniger*); (**b**) *Pristimantis latro* (Oliveira et al. 2017) (from *Pristimantis* gr. *conspicillatus*); (**c**) *Adenomera andreae* (Müller 1923); (**d**) *Adenomera* gr. *heyeri*; (**e**) *Leptodactylus* aff. *knudseni*; (**f**) *Boana cinerascens* (Spix 1824); (**g**) *Boana*

gr. *masniger*, *C. amazonicus*) and medium (e.g., *B. cinerascens*) body-sizes, from flooded (e.g., *B. cinerascens*, *B.* gr. *albopunctata*) and non-flooded forests (e.g., *R. magnussoni*, *A.* gr. *heyeri*), and with terrestrial (e.g. *A. andreae*, *A. angulatus*) and arboreal habits (e.g., *B. cinerascens*, *B.* gr. *albopunctata*). The only taxa lacking examples of riverine-congruent divergences were those large-bodied (e.g. *O. taurinus*, *P. plica*), which may result from increased dispersal, and hence flow of individuals and genes, between banks. These results reinforce how idiosyncratic the diversification of distinct functional groups in association with Amazonian rivers can be (Fouquet et al. 2015; Moraes et al. 2016), especially in areas of highly dynamic landscape history. Still, additional sampling is needed to confirm if this observation is widespread in large-bodied organism.

All focal taxa with reciprocally monophyletic haplogroups on distinct river banks were submitted to temporal analyses, using published rates of substitution to time-calibrate the mitochondrial gene trees (see details in methods at Supplementary Material in online version of this chapter). We recovered a continuous range of riverine-associated divergence times, which we group in three main time periods for discussion purposes: (1) ancient divergences, dating from the middle Miocene (ca. 10 Ma; *C. amazonicus*); (2) divergences in the late Miocene-Pliocene (ca. 5–3.5 Ma; *A.* gr. *masniger*, *A.* gr. *heyeri*, *B.* gr. *albopunctata*, *P.* gr. *conspicillatus*, and *A. angulatus*), and (3) more recent divergences, dating to Pleistocene (ca. 2–1 Ma; *A. andreae*, *R. magnussoni* and *B. cinerascens*; Fig. 25.8).

6 Landscape Evolution and Diversification at the Tapajós River Basin

Our review described how the Tapajós River basin landscape would have varied through time, and our molecular results, allied to other published data, are consistent with a hypothesis that this dynamism shaped the multiple diversification histories of its native biota. This biological impact of landscape dynamism of the basin is also in agreement with its high number of endemic taxa, such as the amphibians *Allobates tapajos*, *A. magnussoni*, *B. tapajonica* and *R. magnussoni* (Lima et al. 2007, 2014, 2015; Brcko et al. 2013; Maia et al. 2017), several undescribed taxa (authors, pers. obs.), the lizard *G. tapajonicus*, the birds *L. vilasboasi* (Barrera-Guzmán et al. 2017; Dias et al. 2018) and *Thamnophilus nigrocinereus huberi* (Zimmer and Isler 2019), the monkey *Mico leucippe* (Pimenta and Silva Jr. 2005) and other mammals (Oliveira et al. 2016), besides several taxa of alluvial trees (Ferreira et al. 2013). In

Fig. 25.5 Focal amphibian and lizard taxa from the banks of Tapajós River, and studied here (**a**) *Rhinella* gr. *margaritifera*; (**b**) *Rhinella magnussoni* (Lima et al. 2007); (**c**) *Bolitoglossa tapajonica* (Brcko et al. 2013); (**d**) *Arthrosaura reticulata* (O'Shaughnessy 1881); (**e**) *Cercosaura* gr. *ocellata*;

addition, other bird, mammal, amphibian and reptile taxa have their current distributions delimited by the rivers within this basin (Cracraft 1985; Ayres and Clutton-Brock 1992; Ávila-Pires 1995; Silva et al. 2002; Moraes et al. 2016).

By analyzing the evolutionary histories of amphibians and lizards, we found a nearly continuous pattern of Plio-Pleistocene-centered divergence dates for taxa that currently occupy opposite margins of the Tapajós. These dates are older than most splits recorded for upland understory birds, which occurred mainly during the Pleistocene (Ribas et al. 2012; Silva et al. 2019). Amphibians and reptiles have lower dispersal abilities when compared to birds, present a strong association with landscape changes, and may retain older historical signals in their genetic profiles. The final uplift of the Brazilian Shield took place during the Late Miocene-Early Pliocene transition (7–5 Ma) (Del'Arco and Bezerra 1989), and this uplift is a known driver of diversification in amphibians and reptiles (Werneck et al. 2012b). We propose that the older splits inferred for some of the taxa analyzed here indicate changes in river courses that may have occurred by terrain adjustments during the uplift (10–3.5 Ma), segregating or gathering biological populations along the different areas of the flooding gradient created in their banks. Subsequent course rearrangements generated by neotectonic events, and changes in permeability due to climatic variations that altered water levels, could have maintained gene flow in some populations or extinguished some taxa due to stronger climatic instability in this region (Irion et al. 2006, 2010; Wang et al. 2017). Recolonizations from the climatically stable western Amazonia, and recent interruptions of gene flow associated with the higher water level of the system, may have driven the other, most recent splits detected in species of birds (Ribas et al. 2012; Silva et al. 2019), and may explain the more recent diversification events inferred here for some of the amphibians (2–1 Ma). Previous studies of vicariant diversification across the Tapajós River were similarly unable to detect synchronic responses to a single historical event—and found a signature of reticulated diversification in lineages isolated on opposite banks (Haffer 1997; Weir et al. 2015; Barrera-Guzmán et al. 2017; Dias et al. 2018; Pulido-Santacruz et al. 2018), with several periods of interruption and reconnection of gene flow (Naka and Brumfield 2018). As explained below, however, vicariant diversification is one of the several alternative hypotheses that may explain the genetic patterns we observed.

The fact that the Tapajós River runs through an ecotonal zone magnifies the landscape dynamism of the Tapajós River basin over time, certainly influencing the biotic diversification in this region (Moraes et al. 2016). Geologically and climatically dynamic zones are known to increase diversification through allopatric speciation and by presenting new opportunities for ecological adaptation (Hoorn et al. 2013; Tuomisto et al. 2016). Taxa with range edges in this ecotonal zone may be especially affected by the rise of a riverine geographical barrier (Moraes et al. 2016). However, recognizing diversification events determined by ecological barriers is a challenge, because such events generate evolutionary signatures with less evident

Fig. 25.5 (continued) (**f**) *Alopoglossus angulatus* (Linnaeus 1758); (**g**) *Chatogekko amazonicus* (Andersson 1918); (**h**) *Plica plica* (Linnaeus 1758). Photographs by Leandro Moraes
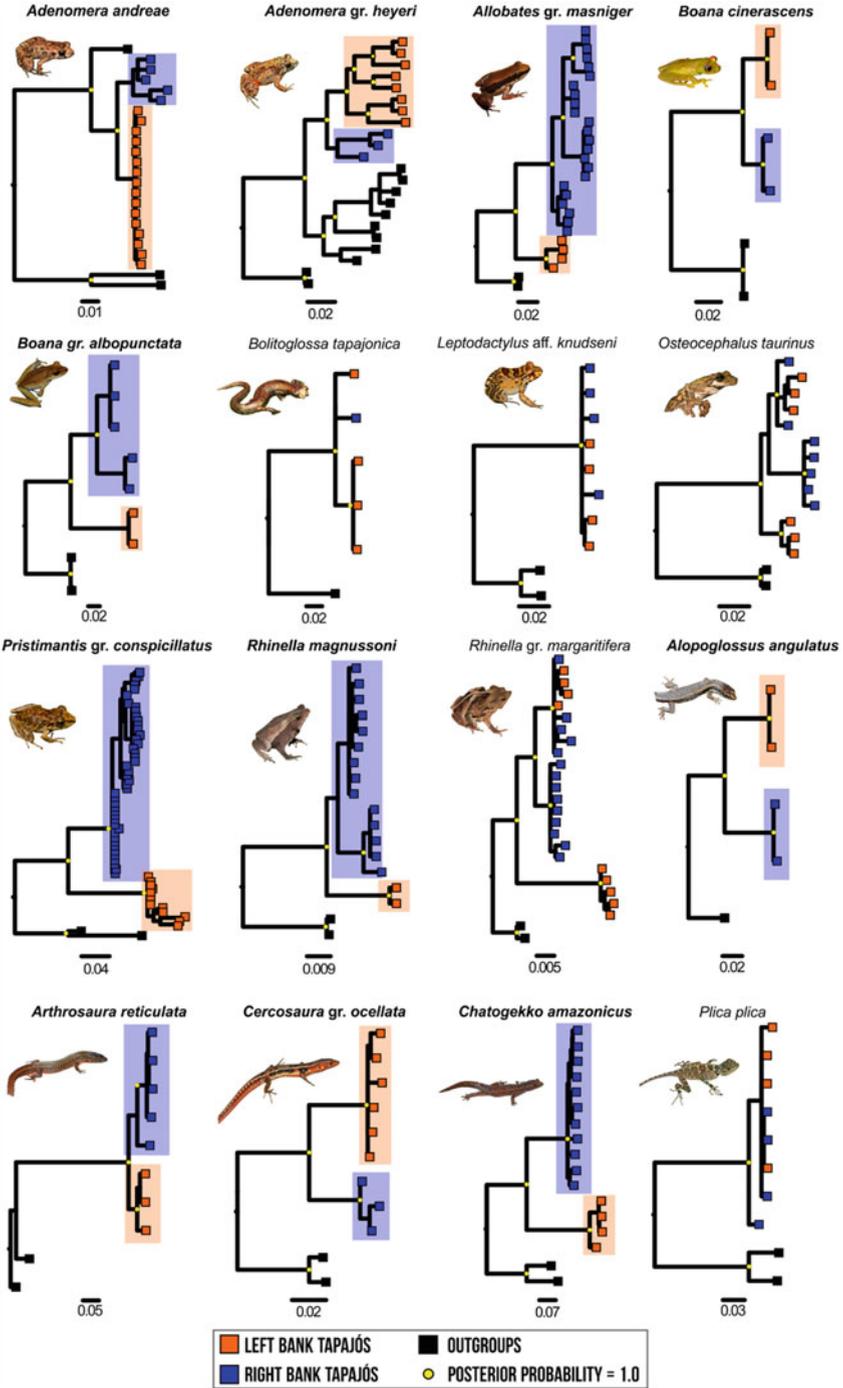
Fig. 25.6 Bayesian phylogenetic gene trees based on mtDNA variation in 16 focal taxa (*16S + COI* for amphibians and *16S + ND4* for lizards), indicating haplotype occurrence across distinct banks of

limits (Ortiz et al. 2018), compared to diversification determined by physical barriers. We propose that taxa with putative origin center centered in the western or the eastern Amazon, and which have their range edges in this ecotonal zone, may have been particularly impacted by ecological diversification combined to the emergence of the Tapajós River. Among the taxa analyzed here, *A.* gr. *masniger* is centered in the west (Tsuji-Nishikido et al. 2012), *B.* gr. *albopunctata* and *A.* gr. *heyeri*, are centered in the east (Fouquet et al. 2014; Pinheiro et al. 2018), and *C. amazonicus* has western and eastern divergent lineages (Geurgas and Rodrigues 2010) and may have been affected by the emergence of a geographical barrier in the ecotonal zone. Other examples may include taxa restricted to the middle Tapajós River, such as *L. vilasboasi* (Barrera-Guzmán et al. 2017), *G. tapajonicus* (Ribeiro-Júnior 2015b), and an undescribed taxa of *Cercosaura* Wagler, 1830 (Ribeiro-Júnior and Amaral 2017). Retractions of suitable habitats due to historical climatic variations, as pointed out in the evolutionary history of *L. vilasboasi*, may also have affected the diversification of these organisms in this ecotonal zone, by isolating its populations (Weir et al. 2015). With the expansion of suitable habitats, previously isolated populations would have been reconnected, especially in the basin headwaters, where hybridization zones are historically recognized (Haffer 1997; Weir et al. 2015).

Importantly, however, we cannot discard the occurrence of independent colonization events, or that the patterns we observe reflect secondary contact between formerly isolated lineages (Moritz et al. 2000; Naka and Brumfield 2018). Some taxa showing evidence of secondary contacts include non-sister lineages present in opposite banks of the Tapajós River, such as lizards in the genera *Alopoglossus* (Ribeiro-Júnior and Amaral 2017), *Cercosaura* (Sturaro et al. 2018) and *Chatogekko* (Geurgas and Rodrigues 2010). In fact, the lizard *Chatogekko amazonicus* showed the most ancient divergence across the Tapajós River; and previous studies already revealed a pattern of older split dates within this species and close relatives, compared to other lizards diversification (Geurgas et al. 2008; Gamble et al. 2011), as well as the occurrence of two very divergent lineages in western and eastern Amazonia, which may have the Tapajós River as their distributional boundary (Geurgas et al. 2008; Geurgas and Rodrigues 2010). Contacts between taxa typical of riparian forests, such as *B. cinerascens* and *B.* gr. *albopunctata*, may also be secondary, since the reduction of current gene flow is counterintuitive in these environments known for greater connectivity in relation to non-riparian forests (Moraes et al. 2016; Harvey et al. 2017). As abiotic information is sparse in this erosive region, and given the high dynamism to which the Tapajós river basin was subjected, a greater volume of biotic data and comparative approaches is needed to test for possible co-divergence events and further advance our understanding of the processes involved in the evolution of this landscape and its biota.

Fig. 25.6 (continued) the Tapajós River. Taxa in bold represent those with reciprocally monophyletic haplogroups on each river bank
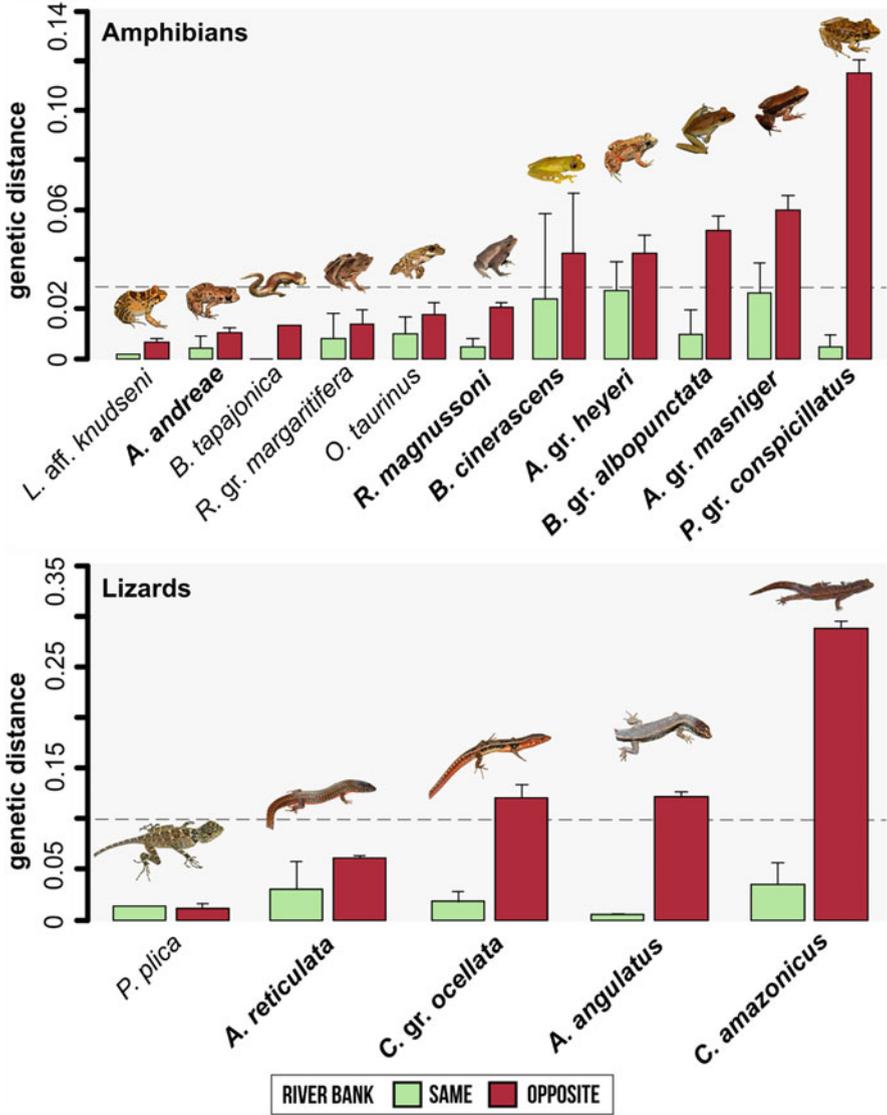
Fig. 25.7 Genetic uncorrected p-distances (mean ± standard deviation) between individuals of the 16 amphibian and lizard focal taxa from same and opposite Tapajós River bank (considering mtDNA gene *16S* for amphibians and *ND4* for lizards). Dashed lines represent known thresholds of interspecific distance for amphibian *16S* gene (Fouquet et al. 2007a, b) and lizard *ND4* gene (Kok et al. 2018). Taxa in bold represent those with reciprocally monophyletic haplogroups on each river bank
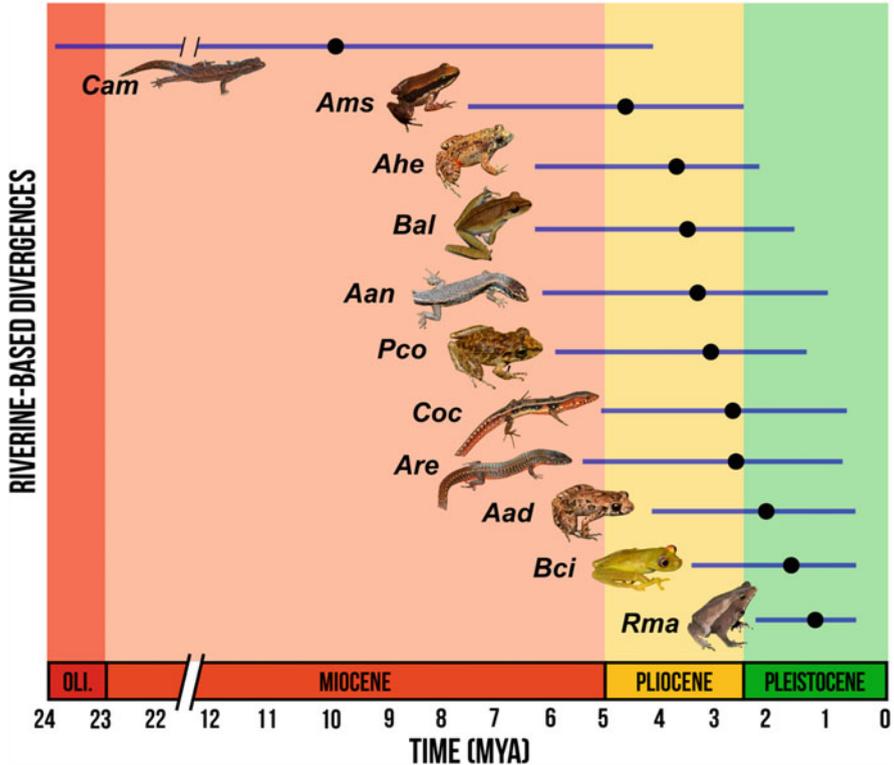
Fig. 25.8 Variation in temporal diversification of focal taxa with distinct lineages between opposite Tapajós River banks, showing divergence times of nodes (median ± 95% HPD) corresponding to current Tapajós River conformation, estimated with BEAST. Acronyms: (Oli.) Oligocene period; (Cam) *Chatogekko amazonicus*; (Ams) *Allobates* gr. *masniger*; (Ahe) *Adenomera* gr. *heyeri*; (Bal) *Boana* gr. *albopunctata*; (Aan) *Alopoglossus angulatus*; (Pco) *Pristimantis* gr. *conspicillatus*; (Coc) *Cercosaura* gr. *ocellata*; (Are) *Arthrosaura reticulata*; (Aad) *Adenomera andreae*; (Bci) *Boana cinerascens*; (Rma) *Rhinella magnussoni*

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