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Authors

Ruokolainen, Kalle
Moulatlet, Gabriel M.
Zuquim, Gabriel
et al.

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Geologically recent rearrangements in central Amazonian river network and their importance for the riverine barrier hypothesis

Kalle Ruokolainen^{1,2,*} , Gabriel Massaine Moulatlet^{2,3} ,
Gabriela Zuquim² , Carina Hoorn^{3,4}  and Hanna Tuomisto² 

¹ Department of Geography and Geology, University of Turku, 20014 Turku, Finland. E-mail: kalle.ruokolainen@utu.fi;

² Department of Biology, University of Turku, 20014 Turku, Finland. E-mail: gabriel.massaine@ikiam.edu.ec; gabzuq@utu.fi; hanna.tuomisto@utu.fi; ³ Universidad Regional Amazónica Ikiam, km 7 Via Muyuna, Tena, Napo, Ecuador. E-mail: m.c.hoorn@uva.nl;

⁴ Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, P.O. Box 94248, 1090 GE Amsterdam, The Netherlands; *Corresponding author: Kalle Ruokolainen, Department of Biology, University of Turku, 20014 Turku, Finland. E-mail: kalle.ruokolainen@utu.fi; phone: +358-505692596

Abstract The riverine barrier hypothesis is a central concept in Amazonian biogeography. It states that large rivers limit species distributions and trigger vicariant speciation. Although the hypothesis has explanatory power, many recent biogeographical observations addressing it have produced conflicting results. We propose that the controversies arise because tributary arrangements in the Amazon river system have changed in geologically recent times, such that large tracts of forest that were on the same side of a river at one time got separated to different sides at another. Based on topographical data and sediment dating, we map about 20 major avulsion and river capture events that have rearranged the river network in central Amazonia during the late Pleistocene and Holocene. We identify areas where past riverine barrier effects might still linger in the absence of a major river, as well as areas where such effects may not yet have accumulated across an existing river. These results call for a reinterpretation of previous biogeographical studies and a reorientation of future works to take into account the idiosyncratic histories of individual rivers.

Highlights

- The river network in central Amazonia has changed radically during the last 100 ky. The river Japurá (Caquetá) disconnected from the Rio Negro and became a tributary of the Amazon only about 1000 years ago, and the upper reaches of both the Juruá and the Madeira have been tributaries of the Purus.
- Shifting tributary arrangements create a dynamic biogeographic landscape where dispersal barriers and dispersal routes for both terrestrial and aquatic organisms are more ephemeral than has been thought.
- The Madeira approximately follows a geological boundary, so species distributional limits might depend either on the riverine barrier effect or on habitat selection. Furthermore, the upper Madeira formerly flowed into the Purus, so the lower Madeira has a shorter history as a large river.
- We provide a map of apparent former positions of four large central Amazonian rivers to encourage the testing of dynamic biogeographical hypotheses.

Key words: Amazon, biogeography, fluvial barrier, geomorphology, Holocene, Pleistocene, rain forest, riverine barrier hypothesis, vicariance

Introduction

Large Amazonian rivers have long been regarded as potential dispersal barriers for terrestrial species (Wallace 1852) and, therefore, promoters of vicariant speciation (Ayres and Clutton-Brock 1992, Ribas et al. 2012). Numerous examples of Amazonian rivers explaining species compositional or genetic turnover can be found in the literature (Fernandes et al. 2012, Ferreira et al. 2017, Lynch Alfaro et al. 2015,

Pomara et al. 2014, Ribas et al. 2012, Schultz et al. 2017). Rivers have also been assumed important boundaries when drawing limits between lowland Amazonian areas of bird endemism (Cracraft 1985) and ecoregions (Olson et al. 2001).

Nevertheless, the biogeographical role of rivers is not a simple issue. Species traits related to life history, behaviour, and dispersal ability affect the degree to which a river can be considered a relevant dispersal barrier in the first place (Dambros et al. 2017, Hayes

and Sewlal 2004). It is also likely that, for many species, such a barrier is semipermeable rather than absolute (Oliveira et al. 2017). In general, it can be expected that the wider the river, the stronger the barrier effect. However, there are several examples of bird species for which the Madeira River is considered a dispersal barrier but the much wider Amazon River is not (Cracraft 1985). Furthermore, existing occurrence data of Amazonian bird species do not support all of the fluvial limits proposed for the areas of endemism (Oliveira et al. 2017). One recent study (Santorelli et al. 2018) even suggests that the Madeira River, the largest tributary of the Amazon, limits the dispersal of a very small proportion of the species in several groups of organisms (snakes, lizards, frogs, mammals, birds, and six groups of insects).

For aquatic species, rivers serve as dispersal routes, and drainage divides as dispersal barriers. Large river catchment basins have been used as geographic units in biogeographic research of fish species (Albert and Carvalho 2011, Hubert and Renno 2006) as well as in the delimitation of aquatic ecoregions (Abell et al. 2008). However, a phylogeographic analysis of about 4,000 fish species (Dagosta et al. 2017) produced a reticulate area cladogram of the Amazonian river catchment areas, implying that their use as basic units in historical biogeography for aquatic organisms is not justified.

The existing data on species distributions in Amazonia is still very patchy (Oliveira et al. 2016, Schulman et al. 2007), which may in itself explain some of the discrepancies between biogeographical observations and the structure of the Amazonian river network. We propose another explanation: the evolutionary scenarios are based on an incomplete model of how the Amazonian fluvial network has formed. In particular, we suggest that some of the large Amazonian rivers have experienced avulsions or river capture events that have changed the positions or tributary arrangements of the rivers much more recently than is generally thought. Such dynamism has been mentioned as a possibly relevant factor in Amazonian biogeography, although without specific scenarios (Albert et al. 2018, Crouch et al. 2019, Dagosta et al. 2017).

At least four river avulsions in lowland Amazonia have been documented that transferred a piece of *terra firme* (non-inundated forest) from one side of a large river to another during the Quaternary. These avulsions happened along the Ucayali River in western Amazonia (Pärssinen et al. 1996) and the Rio Negro, the Amazon and the Madeira rivers in central Amazonia (Almeida-Filho and Miranda 2007, Hayakawa et al. 2010, Ribeiro et al. 2009). However, these events concern such a long time span and so small land areas that they are not sufficient to explain the widespread incongruences related to the riverine barrier hypothesis (aka river barrier hypothesis). Furthermore, avulsions that only shift the river channel without changing the tributary arrangements are irrelevant for aquatic biogeography.

We propose that recent avulsions and river captures are much more widespread and numerous than has previously been appreciated. By documenting and mapping such events, we put forward a framework that can help to re-evaluate distributional and genetic data and thereby build a more coherent picture of Amazonian biogeography.

To address our hypothesis, we systematically searched for geomorphological evidence of river captures and avulsions in Shuttle Radar Topography Mission (SRTM; Farr et al. 2007), which provide an elevation model over Amazonia. Fluvial erosion and sedimentation processes leave behind characteristic topographical patterns in river floodplains (Callander 1978, Salo et al. 1986), and similar marks are commonly found in the currently unflooded terraces adjacent to river floodplains (Latrubesse and Kalicki 2002). Such fluvial marks in the landscape make it possible to identify abandoned river courses until surface denudation erases the topographical signal.

Our aim in this study is to map the possible paleochannels over central Amazonia and to estimate if rearrangements of the fluvial network could have been common and recent enough to potentially play a role in explaining Amazonian biogeography. If the answer to this geomorphological question is affirmative, we will follow up with biological evidence and identify specific predictions that will help future studies to critically test the biogeographical relevance of the changes in the fluvial network. We focus on central Amazonia, where *terra firme* sediments have traditionally been considered to be of Pliocene or early Pleistocene age (Latrubesse et al. 2010). However, recently derived dates (Pupim et al. 2019, Rossetti et al. 2015) suggest that parts of the surface were deposited so recently (late Pleistocene) that the geomorphological structures left behind by paleochannels might still be visible.

Methods

We used the SRTM digital elevation model with 90 m horizontal and 1 m vertical resolution as a source of elevation data to visually search for and map marks of fluvial geomorphology (Fig. 1) in the entire central Amazonian *terra firme* lowlands (Fig. 2) using the QGIS software (QGIS Development Team 2019). Topographical features of presumed fluvial origin were classified into three categories: a) margins of former floodplains, b) traces of river channels, and c) traces of parallel ridges and swales. Each of these is described in more detail below.

The margin of a former floodplain is discernible as a sharp line across which there is a consistent difference in elevation (Fig. 1B, C). Usually on one side of such a line there is an obvious river terrace in which several kinds of fluvial traces are clearly visible, and sometimes a sequence of several terraces adjacent to each other can be seen. In some cases, two sharp and roughly parallel lines can be deduced to delimit a former floodplain, although hardly any fluvial structures are visible between them (Fig. 1C). Such structures have already been interpreted as former river floodplains in earlier geological studies (Hayakawa et al. 2010). Some

of them may lack internal fluvial marks because the corresponding floodplain position was so short-lived that the river channel did not have time to develop its meanders into full sinuosity.

The most obvious traces of river channels are topographic patterns caused by meanders and oxbow lakes (Fig. 1D). The larger the water discharge of the river, the larger the radius of its meanders (Callander 1978). Therefore, it is possible to make reasonable

estimates of the sizes of past rivers by comparing the fluvial marks they have left behind with those of current rivers. Given that a river channel represents the locally lowest topographical position, the channels abandoned by major rivers usually serve as drainage outlets for smaller rivers and creeks, which consequently develop their smaller meanders within the larger paleomeanders (Fig. 1D). The floodplains of such small rivers inherit the broader-scale sinuosity of the

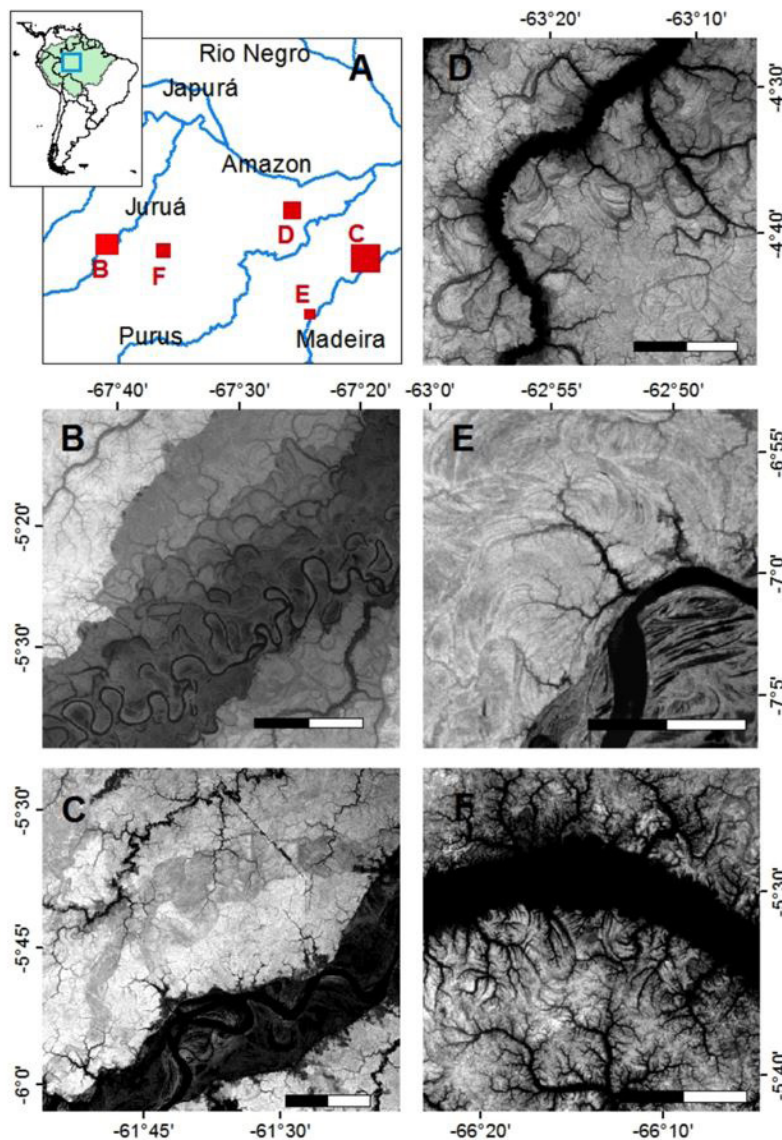


Fig. 1. Types of traces of fluvial activity in central Amazonian *terra firme* (non-inundated) terrain as seen in the shuttle radar topography mission elevation model (SRTM). The scale bar in each panel is 10 km. **A** Index map. **B** Limits between river terraces are visible as sharp boundaries between topographically different levels, with the lower (younger) levels typically bearing traces of meanders and/or ridge-swale sequences. **C** A relict channel is visible as a long band of low-lying terrain north of the current river. We interpret this avulsion to have been so short-lived that the meander loops did not have time to completely close in on themselves and form oxbow lakes before the floodplain migrated again. **D** Curved depressions in *terra firme* correspond to abandoned meander loops of rivers that were considerably larger than those currently occupying them. **E** Parallel sequences of depressions and ridges in *terra firme* indicating scroll bars left behind by laterally advancing past river channels, similar to the ones in the current floodplain in the bottom-right corner. **F** Local drainage following the ridge-swale system and old meander loops of a large river that flowed on the southern side of the present west-to-east oriented blocked-valley river.

Table 1. A breakdown of the number of endemic bird taxa in three Amazonian areas of bird endemism (Cracraft 1985) making two pairs, Inambari vs. Rondônia and Inambari+Napo vs. Rondônia, for which the Madeira River forms a mutual limit. The Rondônia area of endemism is on the eastern side of the Madeira river. The numbers are summed from the data presented in the Supplementary Table 1.

Area of endemism	Number of taxa (species or subspecies, modern areas of distribution from the Cornell Lab of Ornithology and GBIF)					
	Listed by Cracraft (1985)	The Madeira River not relevant as a dispersal barrier for the taxon		Reported to cross the Madeira River		Not known to cross the Madeira river, in parenthesis taxa with ≤ 20 geolocated records in GBIF
		Specialisation on floodplains	Area of distribution far from the Madeira River	Cornell Lab	GBIF	
Inambari	56	2	29	4	7	14 (12)
Inambari+Napo	84	10	35	18	7	14 (5)
Rondônia	21	0	1	0	7	13 (10)
Sum	161	12	65	22	21	41 (27)

paleomeanders of the larger river. This can be seen in the topography until the outline of the paleochannel fades due to surface denudation.

Alternation between parallel ridges and swales emerges when a meander loop grows laterally by eroding the shore at its outer edge and depositing sediments at its inner edge (Fig. 1E; Salo et al. 1986). These scroll-bars are topographically less pronounced than meander loops, so erosion and denudation destroy them more rapidly. However, in some cases the ridge and swale structure can remain visible even after the original topographical variation has faded away. Then the scroll-bars are indicated by numerous parallel streams showing the positions of the past swales (Fig. 1F).

The bird data for the Supplementary Table S1 (summarised in Table 1) were compiled from GBIF on the 19th of April 2019. We searched bird occurrence data for the names used by Cracraft (1985) and for synonyms as listed in Avibase¹. We accepted only those occurrence records that had either four-digit accuracy in the geographical location or those museum collection records that clearly indicated the side of the river.

Results and Discussion

Major river rearrangements

We found evidence of meander loops, ridge and swale topography, and terrace margins (Fig. 1) in many areas in central Amazonia that are currently *terra firme*. Such geomorphological evidence allowed us to map 20 paleochannels of the rivers Japurá, Juruá, Purus,

and Madeira (Fig. 2). North of the Amazon river, the rivers Japurá and Rio Negro are connected by seven relict channels (Fig. 3A and Figs. S1–S7, see also S21 for an index map for all the supplementary figures) that have similar channel width and sinuosity as the present-day Japurá, suggesting that the Japurá has previously been a tributary of the Rio Negro.

South of the Amazon, we identified relict fluvial marks that correspond to the channel width and sinuosity of the present-day Juruá, Purus, and Madeira (Figs. 1F, 3D and Figs. S8–S14). These suggest that both the Juruá and the Madeira have been tributaries of the Purus in the past, with mouths in five different locations, before becoming tributaries of the Amazon (Fig. 2). In addition to these river captures, the locations of eight paleochannels indicate avulsions or places where large areas of *terra firme* have passed from one side of a river to the other without changing the tributary arrangements (Figs. 1C, 2, 3C, and Figs. S15–S18). In two places (on the northern edge of the largest terrace of the Amazon River and between the middle Madeira and Purus rivers; Figs. S19, S20) we also found tracks of fluvial geomorphology corresponding to large rivers far from both present and recent relict floodplains.

Time frame of the rearrangements

Given the absence of sediment samples from the remote interfluvial areas, we deduced the age of river captures and avulsions from a combination of geomorphology and dates from relevant deposits in more accessible areas. Firstly, the abandoned channel between the Japurá and Rio Negro rivers that follows

¹ <https://avibase.bsc-eoc.org/avibase.jsp>, last accessed 20/04/2018

the modern Urubaxi River (Figs. 3A, 3B, and S3) appears to be the youngest paleochannel because it has the best-preserved ridge and swale topography (Fig. 1E). A recent dating is also supported by the account of La Condamine (La Condamine 1813) from the 1740s, describing that during the high-water season it was possible to travel by boat from the Japurá directly to the Rio Negro along the Urubaxi, a connection still identifiable today (Fig. 3A-B). We propose that the connection between the Japurá and Rio Negro broke as recently as ca. 1000 years ago because at that time the lower Rio Negro changed abruptly from a mixed-water to a black-water system (Latrubesse and Franzinelli 2005). Until then, the Rio Negro had transported a heavy suspension load of Andean origin, which made the forming of the Mariuá and Anavilhanas archipelagos possible (Latrubesse and Franzinelli 2005). The white-water Japurá River would be a logical source for those Andean sediments until it was rerouted and started to bring its suspension load directly into the Amazon.

On the basis of topographical clarity, another relatively young paleochannel is the easternmost one of those connecting the present-day Madeira and Purus rivers (Figs. 3D and Fig. S12). It is situated within an upper terrace of the Madeira River that

has been radiocarbon-dated at minimum 32 ka old (Rossetti et al. 2014), and the fluvial traces of the relict floodplain appear more blurred than those of the lower terrace dated to 14–26 ka (Rossetti et al. 2014). In addition, fluvial morphology in the relict floodplain has a similar degree of clarity as the river meanders on a terrace along Purus, which has been inferred to be at most 19 ka years old based on radiocarbon dating (Latrubesse and Kalicki 2002). On these grounds, we estimate that the paleochannel was abandoned between 14 and 32 ka ago. This would have led to a considerable decrease in the water volume of the lower Purus and a corresponding reduction in its ability to act as a dispersal barrier. On the other hand, conducting the waters to the drainage system we now know as the lower Madeira created a large river and hence a potentially important dispersal barrier through an area where the rivers were previously much smaller.

We can infer maximum ages for two additional river capture events based on existing sediment datings using the optically stimulated luminescence method (OSL). The lowermost avulsion channel of the Purus River (Fig. 2) must be less than ca. 63 ka because that is the age obtained (Pupim et al. 2019) for a sample from an upper terrace surface that the paleochannel traverses ca. 10 km east of the town Coari (Fig. S16).

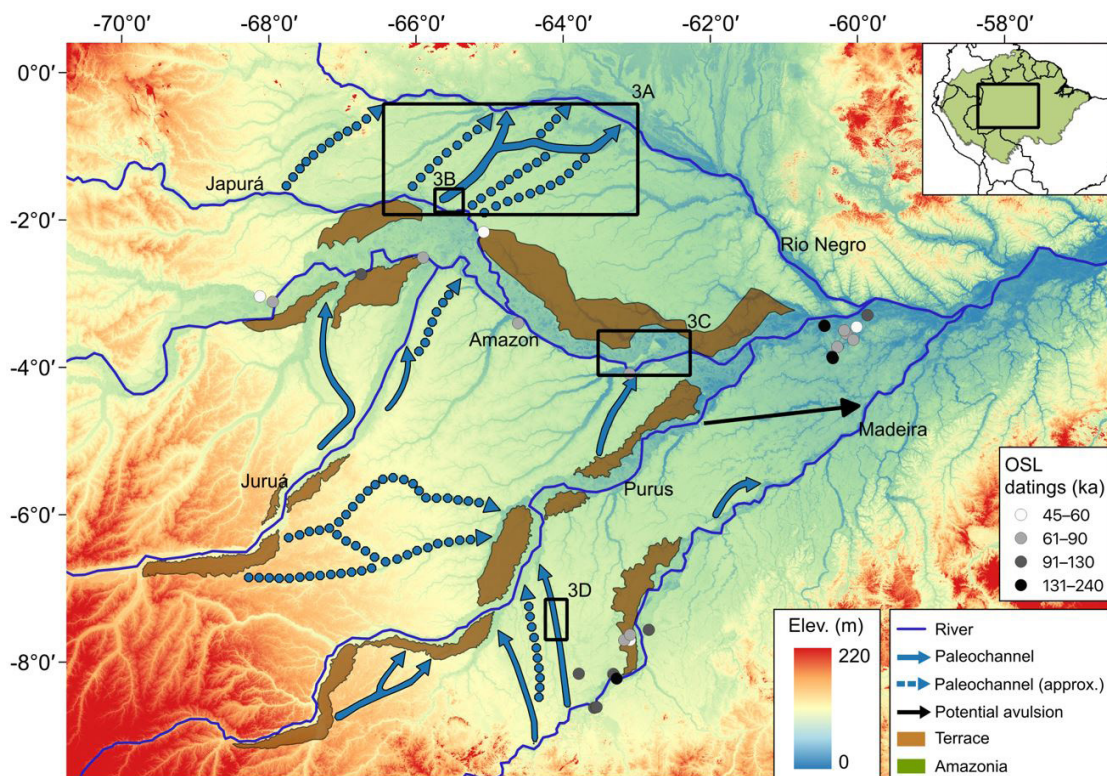


Fig. 2. Approximate routes of major avulsions within the last ca. 100 kyr of the rivers Japurá, Juruá, Purus and Madeira in central Amazonia based on marks of fluvial activity in present-day *terra firme* surface. The clearest fluvial marks, corresponding to more recent locations of the river channels, are indicated with solid lines and routes of higher uncertainty and greater age with dashed lines. The black solid arrow indicates where a future river capture might take place if recent tectonic trends continue. Major river terraces are highlighted in brown. The dots indicate places where sediment samples have been OSL dated (Pupim et al. 2019, Rossetti et al. 2015, Gonçalves Júnior et al. 2016). The numbered boxes refer to the corresponding figures.

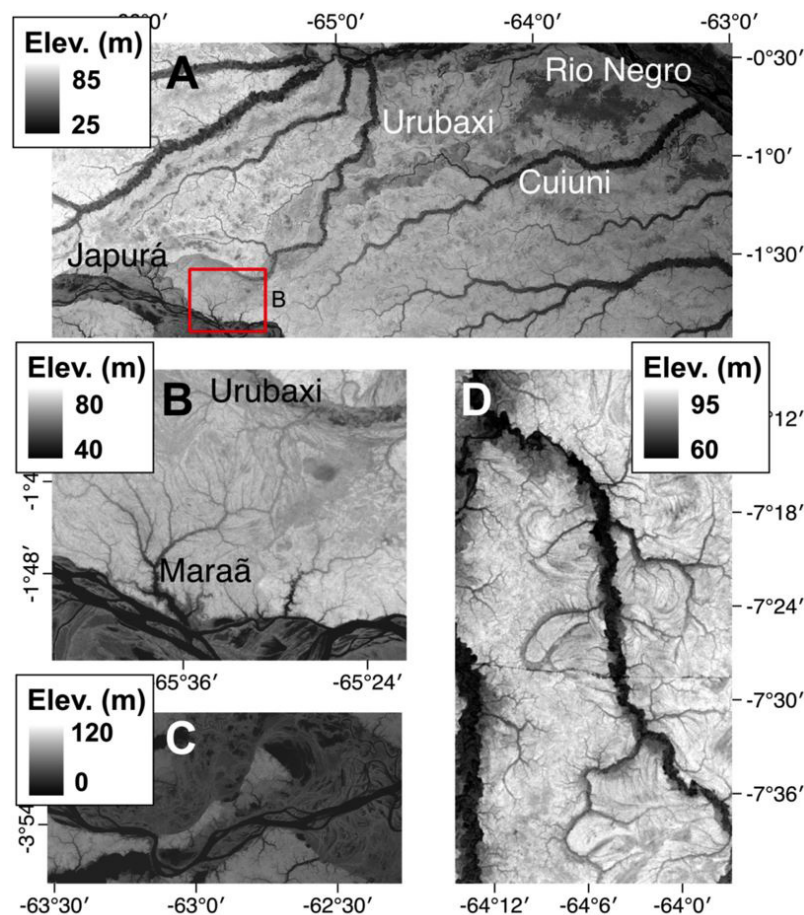


Fig. 3. Three examples of late Pleistocene–Holocene fluvial activity in central Amazonia. **A** Two relatively young paleochannels (with shared upper reaches) connecting the Japurá with the Rio Negro. Currently these paleochannels are occupied by the Urubaxi and lower Cuiuni rivers. **B** The connection between the rivers Urubaxi (tributary of the Rio Negro) and Marã (tributary of Japurá). **C** A recent southward avulsion of the Amazon River channel that caused a 55-km-long stretch of *terra firme* to shift from the southern side of the river to its northern side. **D** Close-up along the river Açuã (tributary of the river Mucuim on the western edge of the map) of past meander loops of the paleo-Madeira from the time when it was flowing into the Purus in the north. The base map in all panels is the SRTM digital elevation model.

Similarly, the maximum age of the paleochannel that connects the Juruá River northwest to the Jutaí River (Fig. S8) is ca. 92 ka as the paleochannel traverses a terrace with that dating (Pupim et al. 2019).

Additional 27 OSL datings for *terra firme* sediments within our study area are relevant (Fig. 2; Pupim et al. 2019, Rossetti et al. 2015, Gonçalves Júnior et al. 2016). One of them comes from a surface that carries marks of fluvial geomorphology and has been aged to ca. 45 ka. Three other samples with ages between 54 and 70 ka come from a surface with obvious fluvial geomorphology: the low terrace of the Madeira has, according to radiocarbon datings, an age of 14–26 ka (Rossetti et al. 2014). The older ages given by OSL are expected as they come from depths of 4.8–7.2 m below the surface. The remaining 23 samples represent surfaces without obvious fluvial geomorphology, and they have been dated between 48 and 240 ka. Overall, the available dates suggest that the fluvial geomorphology can remain discernible in *terra firme* for at least 50 ka, and perhaps up to 150–200 ka.

Accordingly, we propose that the ten topographically clearest paleochannels that we have mapped (Fig. 2) have probably been abandoned within the last 50 ka and almost certainly within 100 ka. The more blurred paleochannels are probably between 50 and 150 ka old and unlikely to be more than 200 ka. These estimates are necessarily rough as they are partly based on a visual interpretation of the degree to which fluvial geomorphology has been eroded. Some of the surface ages may be overestimates: 18 of the 29 OSL datings cited here (Pupim et al. 2019, Rossetti et al. 2015) come from samples taken at depths between 1.7 and 9.4 m, so the actual surface is likely to be younger.

Biogeographical implications

The age of the river captures and avulsions is an important factor determining their relevance for understanding modern biogeographic patterns in Amazonia. If the rearrangements of the fluvial network took place before the majority of present-day species evolved, their barrier effect would have faded by now.

The younger the rearrangements, the more important it becomes to include the historical river positions in explanations of biogeographical patterns.

All the channel avulsions and river captures we mapped have taken place within a time span that is short in terms of species evolution. Accordingly, many *terra firme* species could have gradually dispersed over large parts of central Amazonia into areas that are now separated by major rivers without any single individual having crossed those rivers. This can explain why some studies have failed to find dispersal barrier effects along the Juruá, Purus, and even Madeira rivers (da Silva and Patton 1998, Fernandes et al. 2012, Ribas et al. 2012, Santorelli et al. 2018): the rivers have been so mobile that there has not been sufficient time for dispersal barrier effects to accumulate in any one location or at least along the current river location.

We propose that future studies testing riverine barrier effects in central Amazonia should take into account past channel avulsions and river capture events (Fig. 2). We also suggest addressing two kinds of testable biogeographical predictions for central Amazonian lowlands. Firstly, there should be biogeographical divisions that mirror the historical river courses, at least the most recent ones. For example, the Jaú area of bird endemism (Borges and Da Silva 2012) is limited by large rivers in the north, east, and south but has no obvious dispersal barrier limiting it in the west. We propose that the lower Japurá formed that limit when it still flowed into the Rio Negro (Figs. 2, 3A, 3B, S6). A similar case of vanished barrier may exist between the Madeira and Purus rivers along the route that is currently occupied by the Mucuím River (Figs. 2, 3D, S12). This seems to form a distributional boundary for some species of puffbird (*Malacoptila*; Ferreira et al. 2017) and to be the contact zone between two subspecies of the titi monkey *Callicebus caligatus* (Serrano-Villavicencio et al. 2017). These were possibly separated by the upper Madeira when it still flowed into the Purus (Fig. 2 and 3D).

Our second prediction is that the strength of the dispersal barrier effect of present-day rivers reflects not only channel width and water volume, but also the time that the floodplain has been in its present geographical position. For example, the main channel of the Amazon River is expected to have a strong barrier effect because it has been in approximately the same location dividing lowland Amazonia into northern and southern halves for millions of years (Hoorn et al. 2017). Avulsions that have occasionally caused the channel to move from one side of a given *terra firme* area to the other have not changed the big picture (Fig. 3C) (Ribeiro et al. 2009).

Our results change the established scenario drastically by suggesting that many of the major rivers have been flowing in their current positions for a much shorter time than has generally been assumed. For example, the Madeira River is the most voluminous tributary

of the Amazon and therefore an obvious candidate for an important dispersal barrier. The Madeira has indeed been reported to delimit distributions of several species of birds and other organisms (Fernandes et al. 2012, Ferreira et al. 2017, Godinho and Da Silva 2018, Ribas et al. 2012) and to coincide with the clearest spatial division in species composition of Amazonian birds (Oliveira et al. 2017). However, a recent study (Santorelli et al. 2018) claimed that the Madeira forms a distributional limit for only very few species among several groups of animals. Our results indicate that the lower Madeira, from about the city of Porto Velho downwards, has had its current size for only 14–26 ka. Until then, it was probably too small to trigger allopatric speciation and to constrain species distributions.

In the case of the Madeira, the biogeographical predictions based on the current channel position and the position before the river capture are in clear conflict. This makes the Madeira a very interesting test case (Fig. 2). When evaluating the alternatives, one should also take into account the possibility that the barrier effect of the Madeira is spurious: the river roughly follows the division between the central Amazonian sedimentary plain and the much older craton area of the Brazilian shield. Geologically induced soil differences are known to affect species composition, especially of plants (Higgins et al. 2011, Tuomisto et al. 2016) but also of birds (Pomara et al. 2012) in Amazonian *terra firme* forests. Therefore, a biogeographical transition across the Madeira area may also emerge from habitat differences (Tuomisto 2007, Tuomisto and Ruokolainen 1997).

The biogeographical hypotheses related to the Madeira River are testable given appropriate data since both of the two geological settings can be found on both sides of the river². However, the currently available data on species distributions in this area is too scanty to provide decisive answers even for birds, whose distributions are better known than those of any other organisms in Amazonia. In the mid-1980s, the Madeira River was defined as a limit between the Inambari and Rondônia areas of bird endemism (Cracraft 1985), and 149 *terra firme* species or subspecies of birds were listed as endemic to one or the other area. However, the currently available information on the geographical distribution of these taxa suggests that the limit is far less well defined than this.

According to occurrence data published by the Cornell University³ and the Global Biodiversity Information Facility⁴, for 108 of the 149 endemic taxa the Madeira cannot be a dispersal barrier because either the species do not occur in the Madeira area at all or their distributions include both sides of the river (Table 1). Out of the remaining 41 taxa, 27 are known from 20 or less occurrence points, which means that inferences about their distributional areas, and

2 <https://mapas.ibge.gov.br/tematicos/geologia>, last accessed 09/07/2018

3 <https://neotropical.birds.cornell.edu/Species-Account/nb/home>, last accessed 20/04/2018

4 <https://www.gbif.org/>, last accessed 20/04/2018

whether they are limited by the Madeira river, must be considered tentative.

We believe that the central Amazonian channel migrations reported here (Fig. 2) represent the most recent phase of a considerably longer dynamism that has prevailed since the Amazon River adopted its present west-to-east flow direction, probably in late Miocene–Pliocene times (Hoorn et al. 2017). Tectonically induced tilting in a generally very flat landscape has no doubt been an important factor controlling the fluvial network (Rossetti 2014). Terraces are often asymmetrically positioned along the modern floodplains, suggesting, for example, that the headwaters of the Juruá and Purus have gradually migrated north-westward, whereas the lower reaches of all the major rivers have moved east-southward (Fig. 2). For example, the geologically recent shift southwards of the Amazon River itself has left behind a fluvial terrace that is ca. 700 km long and up to 60 km wide on the northern side of the current floodplain (Fig. 2; Bertani 2015). This may be the largest fluvial terrace on Earth.

Tectonic tilting can be expected to continue, leading to avulsions and river capture events also in the future. For example, the lowermost 150–200 km of the Purus River have relatively recently migrated up to 100 km eastward in two separate occasions. If this trend continues, the Purus may next be captured into the channel of the Rio Preto do Igapó-Açu river, which would make Purus a tributary of the Madeira. The avulsion or river capture events may become more frequent due to climate change and deforestation since these have been predicted to cause an increase in flood intensity in the near future (Barichivich et al. 2018, Guimberteau et al. 2017, Levy et al. 2018).

Our conclusion is that river captures and avulsions of the largest central Amazonian rivers have been frequent and recent enough to complicate biogeographical interpretations of distributional data, including the testing of potential riverine barrier effects. Instead of assuming a fixed network of large rivers since the early Pleistocene, future investigations on the subject should explicitly take into account more recent river avulsions and vanished connections between currently separate rivers.

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Author contributions: K.R., H.T. and G.M.M conceived the original idea; K.R., G.M.M, G.Z., and H.T. collected the data; K.R., G.M.M. and G.Z. led the writing with commenting and reviewing of H.T. and C.H. G.Z. and G.M.M. prepared the figures with input from all authors. All authors have reviewed the paper and the supplementary materials.

Data accessibility statement: The data analysed in the study are available from public sources of United States Geological Survey and Global Biodiversity Facility.

Competing interests statement: There are no competing interests.

Supplementary Materials

The following materials are available as part of the online article from <https://escholarship.org/uc/fb>

Table S1. Occurrence records in GBIF for bird species that are considered endemic to the northwestern or to the southeastern side of the Madeira River.

Figures S1–S21. SRTM images of topographical features that are apparently created by large rivers in areas that currently represent upland terra firme.

Supplementary figures S1–S21 are also deposited as a single file in the Open Science Framework in: <https://osf.io/uwp9n/>

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