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Journal

Biogeographia - The Journal of Integrative Biogeography, 36(0)

ISSN

1594-7629

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Publication Date

2021

DOI

10.21426/B636051761

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Peer reviewed

Monkeys on a free-floating island in a Colombian river: further support for over-water colonization

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Keywords: *Alouatta*, Great American Biotic Interchange, long-distance over-water dispersal, New World monkeys, Panama Isthmus, platyrrhines, rafting dispersal.

SUMMARY

Further to the debate associated with the viability of land-bound mammals being able to colonize remote frontiers by way of long-distance over-water dispersal, observations are documented of monkeys (red howlers, *Alouatta seniculus*) occupying free-standing trees within a large floating island on the Magdalena River in north-west Colombia. Also, we contribute to the discussion related to the 15.0–12.5 Ma (Middle Miocene) arrival of the howler monkeys in Central America, which is well before the Panama Isthmus had fully emerged 3.0–2.8 Ma (Late Pliocene). We speculate it was by way of a raft similar to the ones reported here, possibly from a river entering the sea from northern Colombia.

INTRODUCTION

Practically all of the marine islands host naturally occurring land-locked animals; the small number of exceptions include the Hawaii and Society groups, which are very remote (>3,600 km from the nearest continent) and

geologically young (<6 Ma). Where the sea-bed connecting the insular bodies to a mainland has a depth ≤ 120 m, the general view is that the faunas were assembled due to animals walking in during one of the recent sea-level low-stands associated with a glacial period (over the last 630 ka, the lowest lows in global sea level were

between about 90 and 125 m below the present-day datum; Bintanja et al. 2005). Where the intervening ocean floor is appreciably greater (the average depth of the global ocean is ~3.7 km; Eakins and Sharman 2012), then over-water dispersal is generally invoked, commonly on rafts. Occasionally, though, direct floating is appealed for when the animals are big (e.g. elephants, hippopotamuses; van der Geer et al. 2010, 2015) or have restricted agility (e.g. tortoises; Gerlach et al. 2006). As a consequence, the faunal assemblages on the two sorts of islands are markedly different. With the first (e.g. Bioko, Great Britain, Hainan, Jeju, Taiwan, Tasmania), the suites tend to replicate those on the mainland, with many species, few of which are exclusive to the landmasses (Ali, 2018). With the latter (e.g. Galápagos Archipelago, Madagascar, Mauritius, Seychelles), they are often a highly depleted sub-set comprising hardy, small-bodied organisms, with low energy requirements; some can enter a state of torpor and/or hibernate; endemism is the norm (Ali and Vences, 2019b).

The notion of long-distance over-water dispersal was explored in detail by Matthew (1915) and Simpson (1940), and more recently by Houle (1998, 1999) and de Queiroz (2005, 2014). Recently, however, Mazza et al. (2019) have challenged the idea of mammals colonizing new ground in such a manner. They argue that members of the group are (i) physiologically unsuited to making such trips, (ii) they would have died quickly through starvation and dehydration due to a perceived absence of food and fresh water, and that even if they did survive the crossings then (iii) the genetic bottlenecks associated with a small founder group (gravid individual or a limited number of species members) would make it impossible for the arrivées to establish long-term populations. Ali and Vences (2019a) addressed all three issues and pointed out that the alternative explanation, that is land-bridges, was even more problematic: lack of geological and geophysical evidence corroborating their past existence; such conduits do not strongly

filter those taxa that have access to them; colonizations take place over specific periods, and are thus non-randomly distributed through time; movement is bi-directional.

To contribute to the discussion of the over-water dispersal mechanism, we summarize observations made by two of us (MVR and UF) during a December 2016 fieldtrip to northwest Colombia as part of a collaborative effort involving researchers from the Universidad Nacional de Colombia and the Senckenberg Dresden Museum of Zoology. During the visit, which had a herpetological focus, key information was documented for floating islands both on the mid-course of the Magdalena River and in wetlands within the adjoining El Silencio Nature Reserve, at Yondó municipality, Antioquia Department (Fig. 1).

GEOGRAPHICAL AND CLIMATOLOGICAL SETTINGS

The Magdalena is Colombia's largest river (Restrepo et al. 2006). It extends for 1612 km, with its headwaters located at an altitude of 3685 m above sea level, at the Magdalena 'lagoon', with the main part of its course running between the Central and Eastern cordilleras (Fig. 1). The drainage network is geologically young, and appears to have existed since the late Middle Miocene or early Late Miocene (the boundary between the sub-epochs is dated as 11.6 Ma; Walker et al. 2018) and results from tectonic uplift within the northern Andes (Potter 1997, Hoorn et al. 2010, Anderson et al. 2016, Albert et al. 2018). A key feature of the Magdalena's basin is its vast system of swamps, or 'ciénagas'; there are around 320,000 such patches, and together they have a maximum flooding area in excess of 12,000 km² (Rodríguez and Armenteras 2005). Hydrologically, these swamps play a crucial role in buffering the flow of water across the region; ecologically, the shallow-water bodies are important due to their high productivity (Rodríguez and Armenteras 2005).

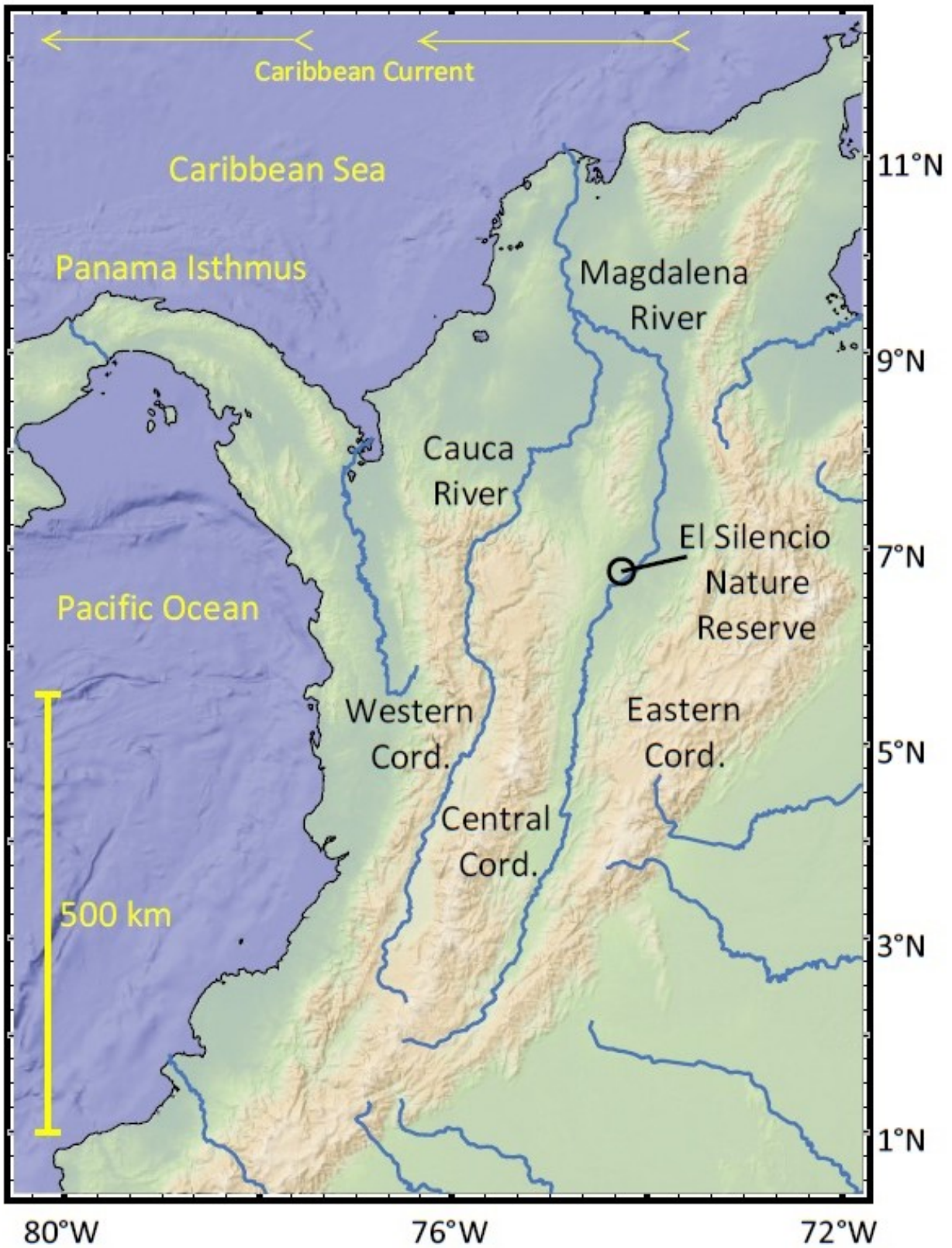


Figure 1. Map showing the course of the Magdalena River, plus other geographical locations and features that are mentioned in the text. The base image was created using *GeoMapApp* (Ryan et al. 2009).

The 320 km² El Silencio Nature Reserve envelops the Ciénagas de Barbacoas on the Magdalena's northwest bank. Centred on 6.73N, 74.28W (Fig. 2) are the two large wetlands, Ciénaga Grande (west) and Ciénaga Pequeña (east) that connect with the Magdalena, their surface elevation being *c.* 90 m (Fig. 2). Within these ciénagas, floating islands are commonplace. They nucleate due to the binding together of submerged and floating aquatic plants including *Eichhornia crassipes* (Mart.) Solms (common water hyacinth), *Ludwigia helminthorrhiza* (Mart.) H. Hara (floating Ludwigia), *Pistia stratiotes* L. (water lettuce), and *Persicaria hydropiperoides* (Michaux) Small (swamp smartweed). As the islands grow and mature, they are then able to harbour large woody vegetation such as *Cecropia peltata* L. (trumpet tree), *Inga* sp. (shimbillo), *Senna reticulata* (Willd.) H. S. Irwin and Barneby (carrion crow bush) and *Euterpe oleracea* Mart. (assai palm) – see Vejarano et al. (2011). During flooding events, rafts from the ciénagas are often flushed out

into the Magdalena where they are then carried downstream. An appreciation of the dynamic nature of this flood-plain ecosystem can be gleaned by inspecting the historical imagery for the area that is available on *Google Earth*, the sequence extending back to January 1970.

In terms of the river's and swamps' discharge states, it is important to note the two main controls (see Angarita et al. 2018). A base-line pattern caused by the annual overhead migration of the Intertropical Convergence Zone results in two rainy seasons: April to May and September to November; two dry seasons typically last from December to February and July to August. Superimposed on this is the multi-year El Niño-La Niña cycle. During the former, the weather belt is pushed somewhat further to the south than is normal and this creates extended drought conditions across the Magdalena's basin. In contrast, during the appreciably longer La Niña phases there can be periods of high rainfall that last a year or more, and this can lead to widespread flooding (e.g. Hoyos et al. 2016).

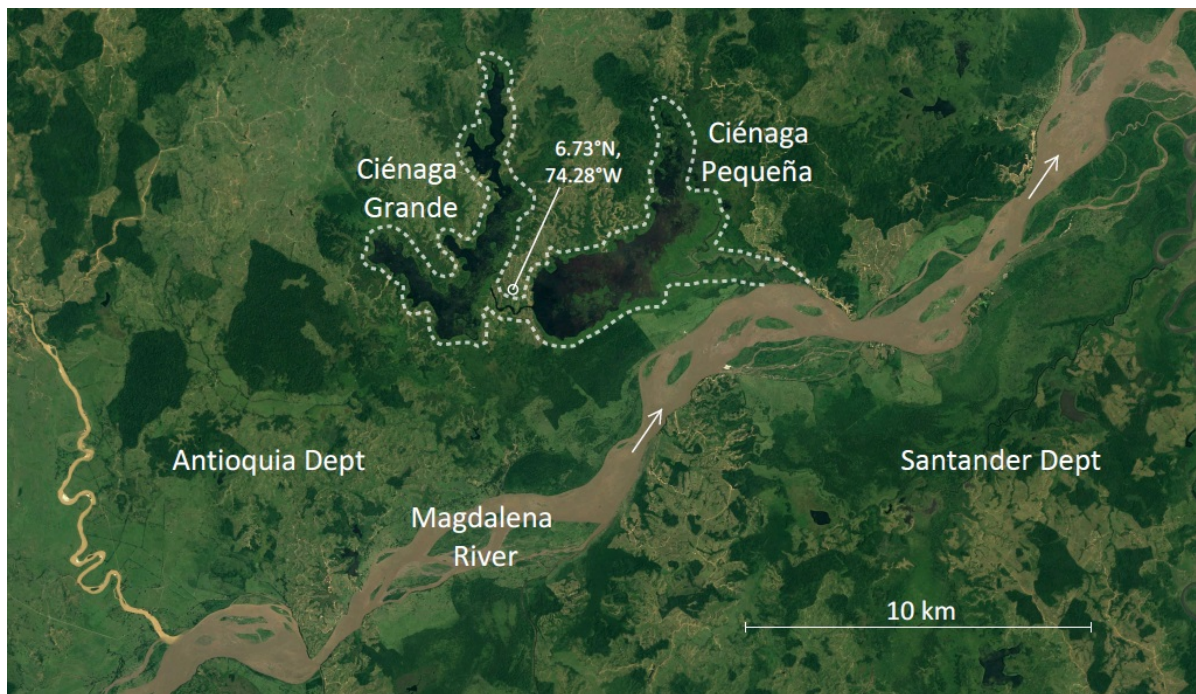


Figure 2. Aerial view of the Magdalena River adjacent to the Ciénagas de Barbacoas where the floating islands were observed. White arrows within the river show the flow direction. The base map is from a *Google Earth* satellite image that was captured on 25 August 2019 (the platform's archive for this area extends back to 1970).

KEY FIELD OBSERVATIONS

During the aforementioned field excursion, there were multiple instances where on the Magdalena we passed drifting islands sporting upright trees, the tallest of which were about 10 metres, the vegetation mats being typically up to *c.* 30 m in length, but some >100 m (Fig. 3). Notably, one had some trees whose crowns were occupied by a troop of the local species of howler monkey, *Alouatta seniculus* (Linnaeus, 1766) (red howler monkey). It is likely that the raft had washed out of the Ciénagas de Barbacoas, but it may have been from upriver. Based on the river conditions, the observed animals, probably alongside other species of ground- and tree-dwelling vertebrates, could have travelled a considerable distance downstream. Notably, they would have had an abundance of food, and with no obvious vertical drops or obstructions along the route some of the rafts may have made it to the lower parts of the Magdalena, and potentially out into the open sea. The critical issue is the recording of a small group of same-species land mammals on a floating island in a wide, free-flowing river.

RELATING THE OBSERVATIONS TO THE MIOCENE PANAMA SEAWAY AND GREAT AMERICAN BIOTIC INTERCHANGE

Developing this further, we note that howler monkeys appear to have originated from their morphologically similar ancestor *Stirtonia tatacoensis* (Stirton, 1951) that existed in what is now the upper reaches of the Magdalena River basin (Stirton 1951, Hershkovitz 1970, Fleagle et al. 1997, Rosenberger et al. 2015). Doyle et al. (2021) hypothesized that howlers from northwest South America crossed into Central America 13.2 Ma (12.5–15.0 Ma) by way of the Panama Isthmus. There is, however, a major problem with this idea because a truly unbroken causeway between South and Central America has only existed since about 3 Ma

(Late Pliocene; Coates & Stallard 2013, O’Dea et al. 2016). Subsequently, there was a massive transfer of land-locked species between the two areas, an event that is known as the *Great American Biotic Interchange* (Marshall 1988, Woodbourne 2010; see also Simpson 1950). To this end, we propose an alternative explanation to the one of Doyle et al. (2021) that involved *Alouatta* colonizing Mesoamerica by way of a floating island similar to those described above. Acknowledging the uncertainties in the Magdalena River’s age of genesis, it is just possible that such a raft departed its mouth in north-west South America close to the Middle Miocene-Late Miocene boundary. In support of this argument attention is drawn to the remote sensing study of Moreno-Madriñán et al. (2015) in which they mapped the pathways of suspended sediment exiting the mouth of the Magdalena. Notably, a sizable fraction of the material is picked up by the Caribbean Current and swept west toward Panama (also see Fig. 1).

CONCLUSIONS

We have provided new information related to the feasibility of over-water dispersal to explain how some land-bound vertebrates have colonized remote locations. Specifically, it involved summarizing observations of a group of medium-sized mammals atop upright trees that were being carried downriver on a floating island in north-west Colombia. Also, we have added to the debate related to the transfer of land animals between the Americas prior to the formation of a fully-connected Panama Isthmus causeway. Finally, we note that if ancestors of the platyrrhine monkeys colonized the Americas by way of a raft that departed Africa in the Middle Eocene (Silvestro et al. 2019), then a Miocene journey by some of their descendants from northwest South America to Central America might in comparison be regarded as being almost inconsequential.



Figure 3. Photograph of one of the floating islands on the Magdalena River during the December 2016 fieldtrip (credit UF). As a scale guide, the raft is about 80 m across. Also note that O'Dea et al. (2016) includes video footage from 2010 of similar scale rafts travelling down the Chagres River in Panama.

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Submitted: 4 February 2021

First decision: 31 March 2021

Accepted: 7 May 2021

Edited by Francesco Maria Angelici