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### Author

Erkens, Roy H.J.

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## The less-splendid isolation of the South American continent

Only few biogeographic scenarios capture the imagination as much as the closure of the Isthmus of Panama. The establishment of this connection ended the “splendid isolation” of the South American continent (Simpson 1980), a continent that had been unconnected to any other land mass for over 50 million years. When the Isthmus rose out of the water some 3 million years ago (mya) the Great American Biotic Interchange started. Since terrestrial biotic interchange was no longer blocked by the Central American Seaway, (asymmetrical) invasion of taxa across this new land bridge transformed biodiversity in North as well as South America (Leigh et al. 2014). Or so the story goes.

A recent paper by Montes et al. (2015) casts further serious doubt on this scenario from a geological perspective. They show that a river system existed, originating in the volcanic arc of Panama and flowing into northern Colombia, about 15 to 13 mya. They base this hypothesis on geological mapping in conjunction with geochronological analyses of river deposits found in northern Colombia. With this they built on previous work (Farris et al. 2011, Montes et al. 2012a,b) in which the hypothesis of a fairly recent closure of the Isthmus was also questioned. Montes et al. (2015) reason that when a river system existed in the Panama-Colombia area, a terrestrial connection needed to be present. Any connection between the Caribbean Sea and Pacific Ocean could only have existed to the west of the current day Panama Canal area, where they postulate the origin of this river system.

So, how do these data fit in with what biologists know about migrations between North and South America? Leigh et al. (2014) provide a comprehensive overview of the historical biogeography of the Isthmus and review for instance that ground sloths had reached North from South America around 10 million years ago and Panama was well populated with all kinds of animals in the Early Miocene (18-19 mya), that fresh water fishes already dispersed in the late Miocene between

lower Central America (Costa Rica) and South America (northern Colombia), and that some snapping shrimp populations were already split long before the Isthmus had finally closed (most between 7–10 mya but some >15 mya). Next to this, several papers showed that plants also migrated between North and South America prior to the closure of the Isthmus (e.g., Erkens et al. 2007, Bacon et al. 2013), although for plants it is difficult to rule out that this happened via long-distance dispersal. Thus, the new findings of Montes and colleagues fit much better with a wealth of evidence from the biological realm that has been amassed over the last years, than the old model of a relatively rapid rise of the Isthmus.

If the land-bridge was available much earlier to many terrestrial organisms, the question that remains, of course, is why they only began to migrate in large numbers between North and South America around 3 mya? The generally accepted scenario that a wide seaway blocked their path is, given the above mentioned studies, not supported. The answer can probably be found in two directions. First of all, the sudden onset at 3 mya is just a remnant from past analyses. As discussed above, earlier migrations indeed have been found and the onset itself of the interchange is placed much earlier than previously accepted (Carrillo et al. 2015), starting already around 10 mya. Although the bulk of migrations might have happened more recently, the onset is more gradual than was postulated. Second, another type of explanation can be found in the type of vegetation present (Leigh et al. 2014), accepting that species ranges can be limited by more than geographic barriers alone (Feeley et al. 2014). Due to climatic cooling around 3 mya a corridor of grassland and savannah allowed open-country animals and some plants to move between North and South America (Molnar 2008, Bacon 2013). Before and after cooling such migration was not possible since tropical forests formed effective obstacles to any migration of these open-country animals. Support for such a scenario is, for instance, provided

by phylogenetic studies on birds of families that are restricted to tropical forests. They have been shown only to move from South to North America after formation of the land bridge and origination of tropical forests (Weir et al. 2009). Further phylogeographic studies in Central America might help to unravel the intricate connections between geology and biogeographic history in the region (e.g., Gutiérrez-García 2013).

To conclude, although the Isthmus might have reached its current shape for the first time around 2.7 mya (Late Pliocene; Molnar 2008), the formation of the land bridge and the onset of the Great American Biotic Interchange is pushed much further back in time than generally thought. This means that the “splendid isolation” of the South American continent is at least 10 million years shorter than originally postulated. This finding is highly relevant since an earlier rise of the Isthmus has profound implications for paleoclimatic modelling of sea currents. These models in their turn impact for instance biogeographic colonisation scenarios of the Caribbean islands and play a role in the understanding the onset of Plio-Pleistocene glaciations (Molnar 2008). Also, estimates of climate are influenced by this finding, determining the availability of suitable habitats for migration, again impacting biogeographic scenarios. Even the way the Andes has formed and our understanding of the wetland origin of the Amazon basin will be impacted by this new finding (Bacon et al. 2013, Hoorn and Flantua 2015). Montes et al. (2015) therefore have made a valuable geological contribution to the further unravelling and understanding of a major biogeographical event.

Roy Erkens

Maastricht Science Programme, Maastricht  
University, The Netherlands  
[roy.erkens@maastrichtuniversity.nl](mailto:roy.erkens@maastrichtuniversity.nl)  
[www.royerkens.nl](http://www.royerkens.nl)

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