Luan Moldan Motta

Sobre a estrutura espacial e temporal do Grande Intercâmbio Biótico Americano em escala local

On the spatial and temporal structure of the Great American Biotic Interchange at local scale

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EXEMPLAR CORRIGIDO

Abstract

The Great American Biotic Interchange (GABI) happened after the connection between North and South Americas was established during the late Neogene with the formation of the isthmus of Panama. A striking resulting pattern was the asymmetrical proportion of mammalian immigrants in each continent, with a higher proportion of northern taxa being found in South America than vice versa. Using mammal fossils occurrences available from an online public database (PBDB) and Generalized Linear Models (GLMs) and Generalized Linear Mixed Models (GLMMs), we tested if there was a spatial structure in the proportion of immigrants in the local assemblages (over 194 total local assemblages) with respect to the distance to the connection between continents. We focused our study on two Pleistocene periods, which allowed us to evaluate if such spatial structure varied with time. We showed that during early stages of the Pleistocene there was a negative relationship between the proportion of immigrants and distance to the point of connection for both North and South Americas. During the Pleistocene later stage a negative relationship was still recovered in North America, however in South America this association faded away. Due to the uncertainties inherent to our data, we did sensitivity analyses regarding the fossil dating uncertainty, the spatial definition of local assemblages, the potential spatial autocorrelation between locations and the potential fossil preservation biases in space. Our results seem qualitatively robust to all sources of uncertainty. We contrast our spatially explicit results to what would be expected at the local scale under the classical hypotheses raised to explain the regional asymmetry in the proportion of immigrants. We advocate that the time for full expansion of immigrants' range is a relevant aspect in structuring the spatial local pattern of immigrants after the GABI but that incumbency, climate, the pool of temperate species, and niche conservatism might also be relevant and more explicitly incorporated in future developments that intend to investigate the local spatial structure of immigrants resulting from the GABI.

Keywords: Macroecology. Fossil record. Mammals.

Resumo

O Grande Intercâmbio Biótico Americano (GABI) ocorreu após a conexão entre as Américas do Sul e do Norte ser estabelecida no final do Neógeno com a formação do istmo do Panamá. Um padrão evidente resultante é a assimetria na proporção de mamíferos imigrantes em cada continente, com maior proporção de imigrantes de origem norte-americana presentes na América do Sul do que vice-versa. Usando ocorrências fósseis de mamíferos disponíveis em uma base de dados online (PBDB) e Modelos Lineares Generalizados (GLMs) e Modelos Lineares Generalizados Mistos (GLMMs), testamos a existência de uma estrutura espacial na proporção de imigrantes nas assembleias locais (mais de 194 assembleias locais ao todo) em relação à distância para a conexão entre continentes. Focamos em dois períodos do Pleistoceno, o que nos permitiu avaliar se tal estrutura espacial variou com o tempo. Mostramos que durante as fases iniciais do Pleistoceno existe uma relação negativa entre a proporção de imigrantes e a distância ao ponto de conexão para ambas as Américas do Sul e do Norte. Durante a fase final do Pleistoceno essa relação negativa foi novamente recuperada para a América do Norte, no entanto na América do Sul essa associação desaparece. Dadas as incertezas inerentes aos nossos dados, fizemos análises de sensibilidade em relação à incerteza na datação dos fósseis, à definição espacial de assembleias locais, à potencial autocorrelação espacial entre localidades e a potenciais vieses no espaço de preservação dos fósseis. Nossos resultados aparentam ser qualitativamente robustos a todas as fontes de incerteza. Comparamos nossos resultados espacialmente explícitos ao que seria esperado ser encontrado em escala local a partir das hipóteses clássicas propostas para explicar a assimetria regional na proporção de imigrantes. Propomos que o tempo para a expansão total da área por imigrantes é um aspecto relevante na estruturação do padrão local de imigrantes após o GABI, mas que incumbência, clima, o *pool* de espécies temperadas e conservadorismo de nicho também possam ter sido relevantes, e que esses aspectos deveriam ser mais explicitamente incorporados em estudos futuros que pretendam investigar a estrutura espacial local de imigrantes resultante do GABI.

Palavras-chave: Macroecologia. Registro fóssil. Mamíferos.

Introduction

Although North and South America are currently connected by the Panama isthmus, and both were part of the supercontinent Pangea during part of the Paleozoic and Mesozoic (Veevers, 2004), they have been isolated from each other for most of Cenozoic. During the end of the Triassic and beginning of the Jurassic, Pangea started to break up isolating the two supercontinents Laurasia and Gondwana (Veevers, 2004), where North America and South America were part of. Also during the Jurassic, the Gondwana supercontinent itself started to break up, leading to the initial stages of isolation of the South American continent. During the Cenozoic, with the formation of the Drake Passage, South America got fully separated from Antarctica and became an isolated continent. The long term southamerican geographical separation allowed its fauna to evolve in isolation for several million years (Simpson, 1950; Chávez Hoffmeister, 2020). This biotic isolation was not absolute, and some taxa such as Caviomorpha rodents and Platyrrhini primates arrived, most likely from Africa as 'island-hoppers' (Simpson, 1950; Poux *et al.*, 2006; Antoine *et al.*, 2012; Chávez Hoffmeister, 2020). Additionally, there are some discussions as to whether or not South America might have had a terrestrial connection with the Caribbean islands (known as GAARlandia for land of Great Antilles-Aves Ridge) during the Eocene-Oligocene transition (Cornée *et al.*, 2021; Ali & Hedges, 2021). Even if this existed it did not last long enough (estimates are around two million years) to promote too much biotic exchange. Therefore the history of South American fauna is indeed one of considerable isolation. North America, in its turn, was part of the supercontinent Laurasia, and through the Cenozoic maintained an active faunal exchange with Eurasia (Webb, 2006; Pires *et al.*, 2015; Silvestro *et al.*, 2015).

The long history of isolation between North and South America began to fade when the Central American Seaway (CAS) started to close during the late Neogene (Webb, 1976; Bacon *et al.*, 2015). The closure had consequences for both the marine and terrestrial biotas, with the division of marine populations on the Pacific and Caribbean coasts (Bacon *et al.*, 2015) and the gradual exchange of terrestrial fauna and flora between continents (Chávez Hoffmeister, 2020). Caimaninae (Chávez Hoffmeister, 2020), terror birds (Phorusrhacidae) (Webb, 1976) and many groups of mammals (Webb, 1976; Marshall *et al.*, 1982; Woodburne *et al.*, 2006) and plants (Cody *et al.*, 2010) took part in this biotic interchange. Although the precise timing of complete closure may be subject of dispute (Bacon *et al.*, 2015), it seems clear (at least for land mammals) that, apart from some herald taxa (Webb, 2006), the bulk of the interchange happened during the Late Pliocene and Pleistocene epochs (Woodburne, 2010).

The interchange of mammals has been particularly well studied, in what is now named the Great American Biotic Interchange (GABI) (Simpson, 1950; Webb, 1976; Marshall *et al.*, 1982). This is in great part due to its relatively more complete fossil record (Simpson, 1950). It is worth emphasizing that the interchange was not a unique temporal event that took place immediately after the formation of the isthmus of Panama but it likely happened in different pulses (Webb, 1976; Woodburne, 2010). The interchange has in fact been systematized in at least four major waves of immigration (GABI 1-4 in Woodburne, 2010). Not only the GABI full development was not instantaneous, but it also did not have symmetrical outcomes, and mammal groups with northern origin contributed more to the southern diversity than vice versa (Marshall *et al.*, 1982). This asymmetry of origin is present both in the past and in the present (Marshall *et al.*, 1982; Carrillo *et al.*, 2020). Around 50% of the mammal generic diversity present in South America is comprised of groups with northern origin, while only 20-35% of genera in North America have southern origin - if excluding Central America, only 10% of North American mammals have southern origin (Marshall *et al.*, 1982, Carrillo *et al.*, 2020).

Several mechanistic hypotheses were proposed to explain this continental asymmetry. Using modern approaches Carrillo and colleagues (2020) recently tested the four main hypotheses present in the literature. The first main hypothesis proposes that North America would have a larger pool of taxa to immigrate, and the asymmetry would arise from this asymmetric pool size (Marshall *et al.*, 1982). Other hypotheses argue in favor of a relatively higher extinction of groups with South American origin (Webb, 1976; Marshall *et al.*, 1982) or that taxa with North American origin would have a higher origination rate (Webb, 1976; Marshall *et al.*, 1982). A fourth hypothesis focuses on the immigration process, proposing that northern groups could migrate at a higher rate than southern groups (Webb, 1976, 1991; Vrba, 1992).

Such hypotheses were formulated to explain the asymmetry measured at a regional scale, usually with no prediction regarding other spatial scales. Even though the interaction between patterns and processes happening at local and regional scales is understood to be relevant in ecology and evolution (Ricklefs, 1987), and previous research suggested that some aspects related to the asymmetry of GABI might not be uniform across space and time (Webb, 1976; Vrba, 1992), no previous study has explicitly investigated the GABI signature at the local scale. More importantly, they did not investigate how the immigration asymmetry might change with respect to the distance to the point of entrance and how this might change over time. Such a scenario might be expected if the immigration process happened in a way similar to a diffusion process, where it takes some time for immigrants to fully expand in space. A few exceptions that touched some of those aspects are worth mentioning.

Webb (1991) recorded the maximum latitude each family reached after invading a continent. He showed that not all groups reached the same latitude, with some being restricted to lower latitudes closer to the connection between continents (Webb, 1991). Marquet and Cofré (1999) analysed mammals' origin and body mass in South America at continental and biome scales, as well as in very few localities, and suggested that on all different scales, a good portion of large mammals have North American origin. They also showed that the proportion of immigrants in the total mammal diversity vary among biomes in South America where some biomes harbour more North American immigrants, while others have a higher proportion of South American natives (Marquet & Cofré, 1999). Carrillo and colleagues (2015) showed that South American fossil assemblages are spatially structured (i.e. close assemblages are more similar than distant ones). Faurby and Svenning (2016) showed that body size and arboreality were good predictors of the distance a taxon could reach after the GABI, which are factors related with the dispersal capabilities of mammal species (Santini *et al.*, 2013). Woodburne (2010) showed that the maximum range of some taxa were not reached immediately, existing a delay in fossils appearing in farther places compared to closer places (the later possibly acting as holding pens). It is expected that biological invasions would not necessarily lead to a large range expansion, or at least not immediate (Stigall, 2019).

A diverse range of mechanisms could influence the spatiotemporal development of the interchange. The climatic and phytophysiognomy distribution on both continents could play a role in who are, and up to where, the migrants reach (Vrba, 1992). The interaction of immigrant taxa with natives could also influence through competition displacement and incumbency effects (Webb, 1976), although such competitive mechanisms have been discarded for cases (Prevosti *et al.*, 2013). Lastly, immigration takes time and different lineages might take different amounts of time to fully expand their ranges as they can have different expansion rates (Grosholz, 1996).

If mechanisms act differently at individual local communities we would expect some spatial structure on the biotic exchange. In fact, Carrillo and colleagues (2018) commented that some sites in northern South America have a higher proportion of native mammals than others sites in the southern portion of the continent. Although this results hints to this possibility of a spatial structure in the asymmetry of the biotic exchange, to our knowledge, no assessment of the GABI asymmetry at local scale was conducted for both continents as a whole.

The goal of our work was to address the question of whether and how the GABI asymmetry in immigrants' proportion was spatiotemporally structured. More specifically, we intended to evaluate if the time that it takes for a genus to fully expand its range could act as a plausible mechanism influencing the GABI's local spatial asymmetry in immigrants' proportion. To do so, we used mammalian fossil occurrences from the Americas compiled in an online database (Paleobiology Database, PBDB) and tested whether there was a relationship between the proportion of immigrants in the local diversity and the distance to the point of connection between the two continents in different periods of time.

Conclusions

1. In this thesis we investigate how the Great American Biotic Interchange might have played out at a local spatial scale. More specifically we look for a spatial structure in the proportion of immigrants with respect to the continents' point of entrance. To our knowledge this is the first time that the immigration asymmetry resulting from the GABI is explicitly studied at a local spatial scale.
2. We used fossil data for all mammal groups available at an online public database, the Paleobiology Database (https://paleobiodb.org/), focusing on the exchange pattern in two moments of the Pleistocene. In that respect we were also able to check if and how the spatial structure pattern changed with time in both continents separately.
3. During the initial stages of the Pleistocene, we showed a negative association between the proportion of immigrants and the distance to the point of entrance between the continents for both South and North America.
4. At a later stage of the Pleistocene we showed that the negative association between the proportion of immigrants and the distance to the point of entrance between the continents fades away in South America but remains present in North America. This temporal effect suggests another layer of asymmetry for the GABI when we compare the two continents. Our results seem qualitatively robust in the light of the incompleteness of the fossil record.
5. We contrast our spatial explicit results to what would be expected by the traditional hypotheses that have been raised to explain the continental asymmetry in the proportion of immigrants. We suggest that time for immigrants to fully expand their ranges is an important mechanism behind the spatial pattern of the proportion of immigrants at a local scale. We also showed that in North America time to expand does not seem to be the only mechanism, and we propose that incumbency, climate, asymmetry in the temperate pool of species, and niche conservatism might also help explain the spatial structure of immigrant proportion and its asymmetry between South and North America.

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