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Distributional patterns of living ungulates (Mammalia: Cetartiodactyla and Perissodactyla) of the Neotropical region, the South American transition zone and Andean region

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ABSTRACT

To recognize the distributional patterns of living ungulates in the Neotropical region, the South American transition zone, and Andean region using the panbiogeographical method of track analysis, and to attempt to correlate these patterns with geological history. The distribution of 24 species of living ungulates (in the families Camelidae, Cervidae, Tapiridae and Tayassuidae) was studied by the panbiogeographical method of track analysis. It was performed using distributional data acquired from literature and databases of scientific institutions. Individual tracks were obtained for each species by plotting locality records on maps and connecting them by minimum-spanning trees. Generalized tracks were determined from the spatial overlap between individual tracks, indicating a common history. The intersection between generalized tracks defined a biogeographic node, implying that these locations are biogeographic composites resulting from different ancestral biotas coming into spatial contact, possibly at different geologic times. The superposition of the 24 individual tracks resulted in five generalized tracks (GTs): GT1, Mesoamerican/Choco (composed of *Mazama pandora*, *Mazama temama*, *Odoicoileus virginianus* and *Tapirus bairdii*); GT2, Northern Andes (*Mazama rufina*, *Pudu mephistophiles* and *Tapirus pinchaque*); GT3, Central Andes (*Hippocamelus antisensis*, *Lama guanicoe*, *Mazama chunyi* and *Vicugna vicugna*); GT4, Chilean Patagonia (*Hippocamelus bisulcus* and *Pudu puda*); and GT5, Chaco/Central west Brazil (*Blastocerus dichotomus*, *Catagonus wagneri* and *Ozotocerus bezoarticus*). The biogeographic node was found in the Northwestern Colombia. The geological events such as tectonism and volcanism that occurred through the Neogene and mainly in the Pleistocene caused fragmentation, diversification and endemism of biota. The biogeographic node in Colombia occurred within a zone of convergence. This node emphasized the complexity of the area and it contains biotic elements with different origins, which represent a special condition for the establishment of priority conservation areas.

1. Introduction

The living ungulates (Cetartiodactyla and Perissodactyla) is an artificial group (O'Leary et al., 2013) and both orders are represented in the Neotropical region, the South American transition zone and the Andean region (*sensu* Morrone, 2006) by 11 genera and 26 species. The occurrence of these species in South America is related to the so-called biogeographic event Great American Biotic Interchange (GABI), which occurred in the Pliocene-Pleistocene boundary (ca. 2.7 Myr), due to the emergence of the Isthmus of Panama (e.g., Woodburne, 2010). Therefore, this is considered the only historic event that shaped the distribution of living ungulates in the above-mentioned regions (Webb, 2006).

Studies in Historical Biogeography attempt to integrate biogeographic patterns and geological history of the Earth in order to understand the evolution of taxa in space and time (see for instance Morrone, 2009). However, biogeographic studies applied to explain the distributional patterns of living ungulates are very scarce.

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In addition, methods in Historical Biogeography are important for studying biodiversity conservation (Prance, 2000). Wilson and Mittermeier (2011) pointed out that most of the ungulate species are vulnerable mainly due to fragmentation of habitat.

A very useful method to study distributional patterns and to define conservation areas is Panbiogeography originated with Croizat (1958, 1964) and later developed by Page (1987), Craw et al. (1999) and Echeverry and Morrone (2013). Panbiogeography emphasizes the spatial or geographical dimension of biodiversity and allows a better understanding of evolutionary patterns and processes (Craw et al., 1999).

Recent studies confirm the validity of the method for living (e.g., Candela and Morrone, 2003; Escalante et al., 2004; Cavalcanti and Gallo, 2008; Pires and Marioni, 2011; del Río et al., 2015; Campos-Soldini et al., 2015) and fossil species (e.g., Candela and Morrone, 2003; Gallo et al., 2007, 2013; Miguel et al., 2014). For a comprehensive revision of Panbiogeography see Morrone (2015).

The aim of this study is to recognize the distributional patterns of living ungulates in the Neotropical region, the South American transition zone, and the Andean region using the panbiogeographical method of track analysis, as well as to attempt to correlate these patterns with geological history.

2. Materials e methods

2.1. Data set

Here we selected 24 of the 26 species of living South American ungulates, because two of them are considered domesticated species (*Lama glama* and *L. pacos*). The ungulates in South America represent the orders Cetartiodactyla (Camelidae, Cervidae and Tayassuidae) and Perissodactyla (represented only by the Tapiridae) (*sensu* Wilson and Reeder, 2005). The geographic distribution informations of each of the studied species were obtained from the literature and databases from scientific institutions (e.g., Museu Nacional of the Universidade Federal do Rio de Janeiro). The geographic coordinates of Brazilian municipalities were obtained from the Instituto Brasileiro de Geografia e Estatística (IBGE) (http//www.ibge.gov.br), and the geographic coordinates of Neotropical Mexico, Central America and South America, from the site Global Gazetteer version 2.2 (http//www.fallingrain.com/world). The biogeographic regions considered in this study (i.e., Neotropical region, the South American transition zone and Andean region) followed Morrone (2006). We recognized 1719 localities (Electronic Supplementary Material 1) of South American ungulates distributed in the following decreasing order: Cervidae (853), Tayassuidae (462), Tapiridae (333), and Camelidae (71).

2.2. The panbiogeographical method

The panbiogeographical method of track analysis consists of plotting locality records of different taxa on maps and connecting them using lines following a criterion of minimum distance, resulting in individual tracks.

These tracks are superimposed and the coincidence of them corresponds to generalized tracks (areas of endemism), indicating a common history, that is, the existence of an ancestral biota widespread in the past and later fragmented by vicariant events (geological events/climatic changes). The intersection of two or more generalized tracks defines the biogeographic node implying that different ancestral biotas interrelated, possibly in different geologic times, and formed a composite area (Craw et al., 1999; Heads, 2004). Moreover, the biogeographic node can be characterized as a site of high diversity (Heads, 2004) and, therefore, it can represent an important biodiversity hotspot (Grehan, 1993).

Individual tracks were constructed for each species by plotting localities on maps using the software ArcView GIS 3.2 (Esri, 1999) and connecting them by minimum spanning trees using the Trazos 2004© extension (Rojas, 2007). Generalized tracks and biogeographic nodes were obtained through superimposing and visual inspection of individual tracks and from their intersection, the biogeographical nodes, also using the software ArcView GIS 3.2. They were drawn by hand on maps, using the Geographic Projection. In order to compare our results, we applied the Trazos 2004® extension (Rojas, 2007), in which we selected the individual tracks to identify the generalized tracks, as well as we selected the generalized tracks to identify the node. Each species participated in the formation of only one generalized track (Morrone, 2009).

3. Results

The superposition of the 24 individual tracks (Electronic Supplementary Material 2) resulted in five generalized tracks (GTs) (Fig. 1): GT1, Mesoamerican/Chocó [composed of *Mazama pandora* Merriam, 1901; *Mazama temama* (Kerr, 1792); *Odoicoileus virginianus* Zimmerman, 1780; and *Tapirus bairdii* (Gill, 1785)]; GT2, Northern Andes [composed of *Mazama rufina* (Pucheran, 1951); *Pudu mephistophiles* (de Winton,1896); and *Tapirus pinchaque* (Roullin, 1829)]; GT3, Central Andes [composed of *Hippocamelus antisensis* (d'Orbigny,1834); *Lama guanicoe* (Muller, 1776); *Mazama chunyi* (Hershkovitz, 1959); and *Vicugna vicugna* (Molina, 1782)]; GT4, Chilean Patagonia [composed of *Hippocamelus bisulcus* (Molina, 1782) and *Pudu puda* (Molina, 1782)]; and GT5, Chaco/Central western Brazil [composed of *Blastocerus dichotomus* (Illiger,1815); *Catagonus wagneri* (Rusconi, 1930); and *Ozotocerus bezoarticus* (Linnaeus, 1758)] (Fig. 1; Table 1). The biogeographic node was recognized in the intersection of GTs 1 and 2 in the Northwestern Colombia (Fig. 1).

Certain species did not participate in the composition of any generalized track, some of them due to their wide distribution, such as *Mazama americana* (Erxleben, 1777), *Mazama goazoubira* (Fischer, 1814), *Tapirus terrestris* (Linnaeus, 1758), *Tayassu pecari* (Link, 1785) *and Tayassu tajacu* (Linnaeus, 1758), and other due to their endemism, such as *Mazama bororo* (Duarte, 1996), *Mazama bricenni* (Thomas, 1908) and *Mazama nana* (Hensel, 1782).

4. Discussion

Our results support recent studies, which indicate that the Andes lead most of the diversification events for vertebrates in South America (Santos et al., 2009).

All generalized tracks obtained can be explained mainly by geological events such as tectonism and volcanism, which occurred in Central America and South America.

Most of these tracks indicated a Western pattern of the biota in South America, bounded by the Andean Cordillera, except for GT5, which is a South American Neotropical pattern.

The GT1, named Mesoamerican/Chocó, represents a biota distributed from the Southern Mexico to Northwestern South American (Colombian Chocó regions). The geology of this area was controlled by a complex interaction between South American, Caribbean and Nazca plates (Costa et al., 2006). This distributional pattern can be inferred as a result of the movements along the tectonic fault zones in Central America (Guatemala, Costa Rica and Panama-Chocó Block) and Northwestern South America (Fig. 2). The GT1 is also associated with the Central American Volcanic arc, whose activity was intense since Early Pliocene (Leeman et al., 1994; McMillan et al., 2004).

The GT2, named Northern Andes, represents a biota distributed from the Cordillera Occidental (Colombia) to Northernmost Peru.