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EVOLUTIONARY BIOGEOGRAPHY AND THE REGIONALIZATION OF THE NEOTROPICS: A PERSPECTIVE FROM MAMMALS

Tania Escalante[1] and Juan J. Morrone[2]

[1] Grupo de Biogeografía de la Conservación, Departamento de Biología Evolutiva, Facultad de Ciencias, Universidad Nacional Autónoma de México, 04510 Mexico City, Mexico. [Correspondence: <tescalante@ciencias.unam.mx>]
[2] Museo de Zoología "Alfonso L. Herrera", Departamento de Biología Evolutiva, Facultad de Ciencias, Universidad Nacional Autónoma de México (UNAM), 04510 Mexico City, Mexico.

ABSTRACT. Evolutionary biogeography aims to discover biogeographic patterns exhibited by plant and animal taxa and to assess the historical changes that have shaped the assembly of biotas. One of these biotas is found in the Neotropical region, which has been described, delimited and regionalized by several authors since the 19th century. Important contributions have been made by several mammalogists, who have identified geographic distributional patterns of mammals of the Americas and have contributed to different schemes of regionalization. Biogeographic regionalizations are based on the identification of endemic or characteristic taxa, constituting natural biotic hierarchies that synthesize the evolutionary/ecological history of the areas. According to the most recent biogeographic regionalization, the Neotropical region is composed by three subregions, two transition zones, seven dominions and 54 provinces.

RESUMEN. La biogeografía evolutiva y la regionalización del Neotrópico: una perspectiva desde los mamíferos. La biogeografía evolutiva pretende descubrir patrones biogeográficos exhibidos por taxones de plantas y animales y evaluar los cambios históricos que han moldeado el ensamble de las biotas. Una de estas biotas corresponde a la región neotropical, la cual ha sido descrita, delimitada y regionalizada por numerosos autores desde el siglo 19. Varios mastozoólogos han realizado contribuciones importantes al identificar patrones de distribución geográfica de los mamíferos de América y han contribuido a diferentes esquemas de regionalización. Estas regionalizaciones biogeográficas se basan en la identificación de taxones endémicos o característicos, constituyendo jerarquías bióticas naturales, que sintetizan la historia evolutiva/ecológica de las áreas. De acuerdo con la regionalización biogeográfica más reciente, la región neotropical comprende tres subregiones, dos zonas de transición, siete dominios y 54 provincias

RESUMO. A biogeografia evolutiva e a regionalização dos neotrópicos: uma perspectiva desde os mamiferos. A biogeografia evolutiva visa descobrir padrões biogeográficos exibidos por táxons de plantas e animais e avaliar as mudanças históricas que moldaram a montagem de biotas. Uma dessas biotas é encontrada na região neotropical, descrita, delimitada e regionalizada por vários autores desde o século XIX. Importantes contribuições foram feitas por vários mastozoologos, que identificaram padrões de distribuição geográfica de mamíferos das Américas e contribuíram para diferentes esquemas de regionalização. As regionalizações biogeográficas são baseadas na identificação de táxons endêmicos ou característicos, constituindo hierarquias bióticas naturais que

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sintetizam a história evolutiva/ecológica das áreas. De acordo com a regionalização biogeográfica mais recente, a região neotropical é composta por três sub-regiões, duas zonas de transição, sete domínios e 54 províncias.

Key words: biota, endemism, patterns, provinces, tracks.

Palabras clave: biota, endemismo, patrones, provincias, trazos.

Palavras-chave: biota, endemismo, padrões, províncias, traços.

INTRODUCTION

Evolutionary biogeography integrates distributional, phylogenetic, molecular and paleontological data in order to discover biogeographic patterns exhibited by plant and animal taxa and assess the historical changes that have shaped biotic assembly (Morrone 2009). This can be accomplished in steps. First, biotas are identified and represented on a map as generalized tracks or areas of endemism. The relationships of the biotas are elucidated under a cladistic biogeographic approach, using the available phylogenetic hypotheses of the taxa that they contain. Based on the biotas recognized and their relationships, biogeographic regionalizations are obtained. Cenocrons, the subsets of taxa that share a biogeography history and have dispersed to the area at a given time, can be identified through fossils, phylogeographic hypotheses and molecular divergence dating analyses. If geological data are available, they are integrated to postulate a geobiotic scenario aimed to explain how different episodes of dispersal and vicariance have shaped biotic evolution.

A biogeographical regionalization, the main result of an evolutionary biogeographic analysis, is a hierarchical system that categorizes geographic areas in terms of their biotas (Escalante 2009). Several criteria have been used to propose regionalizations, including biogeographic naturalness, which is based on the distributional patterns of endemic plant and animal taxa (Morrone 2018a). Such distributional patterns correspond to hypotheses of primary biogeographic homology, which allow identifying biotas as sets of spatio-temporally integrated taxa that coexist (Morrone 2009).

Here, we discuss the biogeographic regionalization of the Neotropics and present some biogeographic theories that have been based on mammal taxa. We also analyze the state of the art and the challenges for the next generations of mammalogists.

THE NEOTROPICAL REGION

The first formal definition of the Neotropical region was provided by Sclater (1858), who included the West Indies, southern Mexico, Central America and South America. Two decades later, Wallace (1876) accepted Sclater's scheme, based on bird taxa, and applied it to other vertebrate taxa, promoting its use as an organizing principle of biogeographic inquiry. According to the Sclater-Wallace system, the Neotropical region comprises South America, Central America, and reaches as far north as central Mexico, where it borders the Nearctic region. This system was followed by many zoogeographers and is considered the standard system, especially for authors analyzing the distribution of vertebrate taxa (Cox 2001).

Cabrera and Yepes (1940) proposed a zoogeographic scheme of South America, based on the distribution of mammals. They considered that Sclater's Guianan-Brazilian and Patagonian subregions were characterized by the proportion of species belonging to different mammal orders. The Guianan-Brazilian subregion corresponded to the tropics of South America, predominating the lowlands with forests and savannas. Its southern boundary followed an oblique line that goes from northern Peru to central Argentina. Characteristic mammals correspond basically to Marsupialia, Chiroptera, Primates and Xenarthra. The Patagonian subregion corresponded to the rest of the continent, extending in most of Peru, Bolivia, Argentina and Chile. Sclater (1858) and Wallace (1876) had previously named it Chilean subregion, but Cabrera and Yepes (1940) considered more appropriate to name it Patagonian. They cited characteristic species of Cervidae, Camelidae and Rodentia. Additionally, Cabrera and Yepes (1940) defined 11 smaller divisions named districts, based on physiographic criteria and the presence of mammal species.

Hershkovitz (1969, 1972) provided a review of the mammal fauna of the Neotropics. He recognized the Brazilian, Patagonian and West Indian subregions as distinct, while treating Mesoamerica as a province of the Brazilian subregion. The boundaries of this regionalization are similar to Morrone's (2018b) Andean region + South American transition zone.

Cabrera and Willink (1973) recognized five dominions within the Neotropical region: Caribbean (Mexico, Central America and the Antilles), Amazonian, Guianan, Chacoan and Andean-Patagonian. The Caribbean dominion included the Mountain Mesoamerican, Mexican Xerophyllous, Caribbean and Guajira and Galapagos Islands provinces; the Amazonian dominion included the Pacific Amazonian, Pacific, Yungas, Venezuelan, Cerrado, Paraná, Sabana, Atlantic and Páramo provinces; the Guianan dominion included the Guyana province; the Chacoan dominion comprised the Caatinga, Chacoan, Espinal, Prepunan, Monte and Pampean provinces; and the Andean-Patagonian dominion had the High Andean, Punan, Desert, Central Chilean and Patagonian provinces. Cabrera and Willink's (1973) Neotropical region did not include the southernmost area of South America, which was assigned to the Antarctic region. Although mammals were not especially relevant for the areas delimited by Cabrera and Willink (1973), their scheme has been widely adopted and used for characterizing and naming geographic areas by mammalogists and authors working with other plant and animal taxa.

Müller (1973) analyzed the geographic distribution of Neotropical vertebrate taxa. He identified 40 dispersal centers (equivalent to areas of endemism). For each center, Müller (1973) mapped the distributional areas of several endemic species. Additionally, for some centers, he recognized nested subcenters. Some of the centers and subcenters are coincident with areas recognized by other authors, whereas others represent smaller nested units.

Koopman (1982), based on distributional maps of bats, recognized seven zoogeographic provinces in South America: Patagonian, Eastern Brazilian Highlands and Coast, Amazon Basin, Eastern Slopes of the Northern Andes, Northern Coast and Islands, Pacific Coast of Peru and Northern Chile, and Pacific Coast of Colombia and Ecuador. Koopman (1982) described these provinces based on endemism, and, although he did not use a particular method, he pointed out that the boundaries between these provinces were fuzzy and complex.

Morrone (2014a, 2017), based on the distributional congruence of distributional patterns of plant and animal taxa, considered that the Neotropical region is comprised of three subregions (Antillean, Brazilian and Chacoan), two transition zones (Mexican and South American) and seven dominions (Mesoamerican, Pacific, Boreal Brazilian, Southwestern Amazonian, Southeastern Amazonian, Chacoan and Parana). This scheme included 53 provinces, to which Martínez et al. (2017) added another one (**Fig. 1**). This regionalization excludes Patagonia and the Andean area, which are assigned to the Andean region. (Recently, Roig-Juñent et al. [2018] considered that the Patagonian subregion is not strictly Andean but part of the South American Transition Zone.) Additionally, in the areas of biotic overlap of the Neotropical region with other regions, two transition zones are delimited: the Mexican Transition Zone in the overlap with the Nearctic region and the South American Transition Zone in the overlap with the Andean region. Morrone's regionalization is not even chiefly based on mammals, and some provinces have not been characterized by endemic mammal species.

Fig. 1. Regionalization of the Neotropical region (modified from Morrone 2017).

MODERN AREAS OF ENDEMISM AND GENERALIZED TRACKS

The evolutionary biogeographic approach used here view areas of endemism and generalized tracks as essential to develop regionalization schemes. For the 21st century, there are few published papers on the identification of areas of endemism based exclusively on mammals for the Neotropical region. Escalante et al. (2013) found a large partial pattern of endemism that corresponds to the Neotropical region, which overlapped with the boundaries of the Nearctic region (Escalante et al. 2010), constituting the Mexican Transition Zone. It has been proposed by several authors that the Neotropical region is a complex area with diffuse boundaries. For example, Noguera-Urbano & Escalante (2015, 2017) found that the Neotropical region corresponds to several areas of endemism showing multiple boundaries, suggesting a dynamic pattern. These boundaries exclude the Nearctic and Andean regions (located at the northern and southern limits of the Neotropics) in the strict sense, but at the same time, include areas of overlap in the laxer sense, according to Morrone's (2014a) scheme. Therefore, the core of the Neotropical region is located from Veracruz and the Pacific coast of Mexico to the southern boundaries of the Amazonian forest in Brazil (Noguera-Urbano & Escalante 2017). Escalante (2017) applied the concept of naturalness and based on species, genera and families of mammals, found that the Neotropical region is a large area of endemism with a complex successively nested pattern, including the Mexican Transition Zone, and excluding southern South America, which encompasses both the South American Transition Zone and the Andean region. Finally, Escalante et al. (2018) identified a partial generalized track corresponding to the Neotropics, which includes a very complex nested pattern, beginning in the lowlands of the Isthmus of Tehuantepec in Mexico. This pattern overlaps with a Mesoamerican pattern, generating many biogeographic nodes in the mountain areas of central and southern Mexico.

Within the Neotropical region, some contributions have focused on the patterns of endemism of the mammalian fauna. Ron (2000) analyzed 56 species of primates, in addition to anurans and lizards, to generate a hypothesis of historical biogeography, finding two areas of endemism: Central America-Chocó and Amazon Basin, the latter divided into Upper Amazonia, Guiana and Belém-Pará. Costa et al. (2000) identified areas of endemism for marsupials, rodents and primates, where the Atlantic Forest was recognized as a biogeographic unit, showing a break in the southeastern area around the Serra da Mantiqueira. Sandoval et al. (2010) used bats and marsupials to identify areas of endemism in the Yungas of Argentina, obtaining three generalized areas inside it. Sandoval et al. (2013) developed a similar study in the Chaco, supporting the naturalness of this province based on patterns of endemism of bats. Olguín-Monroy et al. (2013) regionalized the tropical evergreen forests in Mesoamerica with mammals, obtaining areas of endemism in Yucatán-Pantanos de Centla and Tehuantepec-Panamá. Escalante et al. (2013) recognized three patterns of endemism within the northern Neotropics: Pacific Central America, Mexican Gulf-Central America and Central America. Sandoval and Ferro (2014) analyzed the patterns of endemism of 80 species of rodents of northwestern Argentina, finding nine consensus areas grouped into two patterns: southeastern Andean slopes (southern Argentinean Yungas) and southwestern High Andes (Monte Desert). Prado et al. (2015) identified three general areas of endemism for 102 species of oryzomyine rodents in Central and South America: northwestern South America, eastern South America, and northern South America. Noguera-Urbano and Escalante (2015) found 101 areas of endemism using 2,052 mammal taxa (families, genera and species). They identified areas of endemism that correspond to subregions, dominions, provinces and unions and transitions between provinces. In addition, these authors overlapped all areas of endemism finding two transition zones where many boundaries coincide, Central America and Andes, that correspond to the Mexican and South American Transition Zones, respectively (Noguera-Urbano & Escalante 2015; Noguera-Urbano & Ferro 2017).

Regarding generalized tracks, García-Marmolejo et al. (2003) analyzed 97 species of Mexican mammals and found six different generalized tracks which are exclusively Neotropical, mainly located in coastal areas. Gallo et al. (2013) applied a track analysis to species of megafauna of herbivore mammals, obtaining past distributional patterns similar to the recent ones. Absolon et al. (2016) found five generalized tracks for ungulates, two of them representing Neotropical patterns: Mesoamerican/Chocó and Chaco/Central West, whereas the other three are mainly Andean (Brazil Northern Andes, Central Andes and Chilean Patagonia. In addition, Absolon et al. (2016) found a panbiogeographic node in northwestern Colombia.

BIOTIC EVOLUTION

In addition to the identification of biotas and the regionalization of the Neotropics, several authors have postulated theories to explain the biotic evolution of its mammal fauna. One of the first authors was Ameghino (1891, 1893, 1894, 1897a, b, 1900-1903, 1906, 1907), who developed a theory to explain the origin and distribution of South American mammals. He postulated that all mammals originated in Patagonia and dispersed from this area to the rest of the planet in four basic dispersal events: Cretaceous to Australia, Cretaceous-Eocene to Africa, Oligocene-Miocene to Africa, and Miocene-Pliocene-Quaternary to North America. This "extreme Australism" is based on the classical dispersalist approach of Darwin and Wallace. Toward the end of the 19th century and the beginning of the 20th century, Ameghino's theory was criticized and eventually discarded, mainly because the temporal correlations, based exclusively on mammals, were wrong (Morrone 2011).

According to the "New York school of zoogeography" of Matthew and Simpson, South America was originally devoid of mammals and was populated from North America, followed by in situ differentiation that was facilitated by its isolation during the Paleogene. Matthew (1914) postulated that the main lines of migration occurred from Holarctic centers of dispersal toward the south due to climatic changes and cycles of elevation and submergence of land. Also, Matthew (1914) described the dispersal of each order of mammals from the Holarctic region based on the position and size of the boreal areas and the climate. Later, Simpson (1940, 1953) suggested that North America is probably the main source of the old South American fauna. He divided the mammals in faunal strata (Simpson, 1950), regarding the territory occupied at specific times (Early Paleocene, Late Eocene-Oligocene, and Late Miocene to Recent).

Darlington (1957) reviewed mammal distributional patterns of the world. He considered that recent mammals did not exhibit clear patterns, because many taxa have declined rather than radiated recently, but fossil taxa provided clearer patterns. He also discussed transitional faunas between tropical Africa and temperate Europe, between tropical and temperate eastern Asia, between tropical and north-temperate America (= Mexican Transition Zone) and between Eurasia and North America. Analyses of particular taxa provided by Darlington (1957) were mostly based on fossil evidence.

Reig (1981) postulated a series of "horofaunas" to represent the changes of the mammalian faunas in South America. These horofaunas corresponded to assemblages of species that coexist and diversify in a given area during a prolonged time, representing lasting biogeographic units. According to the author, four successive horofaunas may be identified: (1) Gondwanan Protohorofauna: lineages that inhabited the South American portion of western Gondwanaland from Mid Triassic to Late Cretaceous; (2) South American Paleohorofauna: autochthonous lineages that evolved in South America from Late Cretaceous to Late Eocene; (3) South American Cenohorofauna: both autochthonous lineages and lineages that dispersed in successive dispersal events; and (4) Neotropical Neohorofauna: transformation of the previous horofauna with the incorporation of Nearctic lineages through the Panama

Isthmus and dispersal to the north (Central America and southern Mexico).

Koopman (1982) postulated that there was a great interchange of bats of northern South America and Middle America, and between the South American mainland and the northern islands, some of them connected in the late Pleistocene.

Pascual (2006) divided the evolutionary biogeographic history of the South American terrestrial mammals in two great episodes: Gondwanan, represented exclusively by endemic Mesozoic lineages that evolved in Gondwanaland; and South American, represented by endemic taxa that dispersed from North America to South America. Within the latter, Pascual (2006) recognized four stages. The first corresponds to the span between the extinction of the last Gondwananland mammals and the first immigration of Laurasian Marsupialia and Placentalia, as well as the Late Eocene-Early Oligocene dispersal of primates and rodents from Africa. In the second stage (Late Eocene-Early Oligocene) the primitive ungulate mammals were replaced by more modern taxa that dispersed from North America, including Simpson's (1950) "Old Island Hoppers" (monkeys and caviomorphs, which Simpson thought dispersed from North America); and the "Late Island Hoppers", the heralds of the Great American Biotic Interchange, just before the emergence of the Panamanian isthmus that developed when North and South America were isolated. The third stage corresponds to the "Great American Biotic Interchange" (Stehli & Webb 1985). The last stage is the "Megafaunal extinction", that occurred 10 ka ago, and together with the arrival of *Homo sapiens* 13 ka ago, modeled the current composition of the Neotropical mammal fauna. In post-Pleistocene times, the last North American immigrants (probably from Central America) arrived.

Both Reig (1981) and Pascual (2006) have rescued some elements of the Ameghinean theory, representing modern developments of dispersalism that incorporated vicariant events. Their efforts are similar to those of other authors that have integrated dispersal and vicariance explanations (e.g., Halffter, 1987; see also Halffter & Morrone, 2017), going beyond the classic dispersalism of Matthew and Simpson and the extreme vicariancism of Croizat, Rosen, Nelson and Platnick (Morrone 2011). The different biogeographic theories proposed up to the present have considered the existence of episodic dispersal events for South American mammals. Goin et al. (2016) discussed the different dispersal events in the Late Cretaceous-Paleogene of the Metatheria of South America, which involved North America, Antarctica and Australia. Escalante (2017) found contradictory relationships between the Nearctic region and both the Palearctic and Neotropical regions, due to the geological history of the Earth (the Laurasia-Gondwana split) but also as the result of bidirectional dispersal events.

Within the Neotropical region, some authors have postulated different processes to explain the distributional patterns of mammals. Koopman (1982) considered that the vicariance produced by the Andes has not been an effective barrier for bats. For Ron (2000), the isolation of South America during the Cenozoic and the elevation of the Andes were decisive for the patterns of endemism in the Neotropical forests, as well as the separation of eastern and western Amazonia and the early separation of eastern Amazonia south of the Amazon River (Belém) from other areas in the Amazonas Basin. More recently, Patterson et al. (2012) described "cis-Andean" (eastern) and "trans-Andean" (western) mammalian distributional patterns. Some of these patterns could be related to groups widespread before the Andean orogeny and later isolated by the developing of the mountain system, but others represented a more recent dispersal across the Andes, which have acted as a faunal corridor. The results of Absolon et al. (2016) also indicated that the Andes triggered several diversification events for vertebrates.

Morrone (2014b) undertook a cladistic biogeographic analysis to identify the main events in the biotic diversification of the Neotropical region, including seven mammal taxa (*Alouatta*, *Ateles*, *Caluromys*, *Marmosa*, *Metachirus*, *Oryzomys* and *Rhipidomys*). The general area cladogram obtained shows that the Neotropical region constitutes a natural biogeographic unit, with a first split separating the Antilles and a second one dividing the continental areas into a northwestern and a southeastern component. Within the northwestern component the areas split following the sequence: (northern Amazonia, (southwestern Amazonia, (northwestern South America, Mesoamerica))). Within the southeastern component the areas split following the sequence: (southeastern Amazonia, (Chaco, Parana)). The three main components are treated as the Antillean, Brazilian and Chacoan subregions. Dispersal and vicariant events postulated to explain these patterns might have occurred during the Cretaceous, when the Caribbean plate collided with the Americas, a combination of eustatic sea level changes and tectonic deformations of the continental platform exposed large parts of South America to episodes of marine transgressions, and the Andean uplift reconfigured the Amazonian area. Neogene and Quaternary events are assumed to have induced later the diversification within these large biogeographic units.

It is evident that the geobiotic history of the Neotropical mammal fauna is a complex issue, which involves both vicariance and dispersal events. Moreover, recent climatic changes of the Pleistocene and part of the Holocene also have modified drastically the distributional patterns of the mammals in the Neotropics. Pinilla-Buitrago et al. (2018) used species distribution models transferred to three past periods in order to analyze the effect of the climatic changes on the areas of endemism identified for beetles and mammals in the Mexican Transition Zone. They found that some areas of endemism have persisted geographically, but others have changed over the last 130 000 years. In this sense, it is also expected that areas of endemism can change in short times in the future due to climatic changes (Aguado & Escalante 2015).

THE NEOTROPICAL REGION TODAY

Currently, we recognize the Neotropics as a large area of endemism/generalized track corresponding to the hierarchical level of region within the Holotropical kingdom (Morrone 2015). The Neotropical region is composed by three subregions and also includes the Mexican and South American Transition Zones (Morrone 2014, 2017). Placement of the Neotropical region in the Holotropical kingdom emphasizes vicariant events with the Ethiopian and Oriental regions, whereas recognition of two transition zones emphasizes dispersal events with the Nearctic and Andean regions (**Fig. 2**).

Sensu lato, the Neotropics include most of South America, Central America, southern and central Mexico and the Antilles, between 40°N-40° S. Sensu stricto, the Neotropics correspond only to lowland areas from Veracruz and the Pacific coasts of Mexico to the southern limit of Amazonia in Brazil, with a core area located between 20° N-15° S (Noguera-Urbano & Escalante, 2017).

CHALLENGES FOR THE FUTURE

Although there have been several recent efforts to incorporate big databases of distribution and other data (e.g., beta diversity, molecular data, bioclimatic predictions and postdictions, etc.), we still have pending tasks to obtain a detailed evolutionary biogeographic history of the Neotropical mammal fauna. Many areas of endemism previously proposed should be evaluated with other taxa and at different scales to support their recognition. Also, molecular track analysis (Heads 2012) is a promising approach that may help elucidate some aspects of vicariance events occurring within each subregion. It is surprising that in the 21th century, several species of mammals have been discovered and described for the first time (Burgin et al. 2018). Therefore, new species, more complete phylogenies and modern geological theories are needed to improve cladistic biogeographic analyses at the regional level.

Intraspecific phylogeography is another interesting approach that may help refine biogeographic regionalization at the province and district levels. In this sense, ecological, genetic and populational data could be incorporated to delimit the smallest areas of endemism. Moreover, techniques of modeling and prediction of geographic distributional areas, analyzed under solid theoretical bases, may allow us to improve the natural regionalization of the Neotropical region.

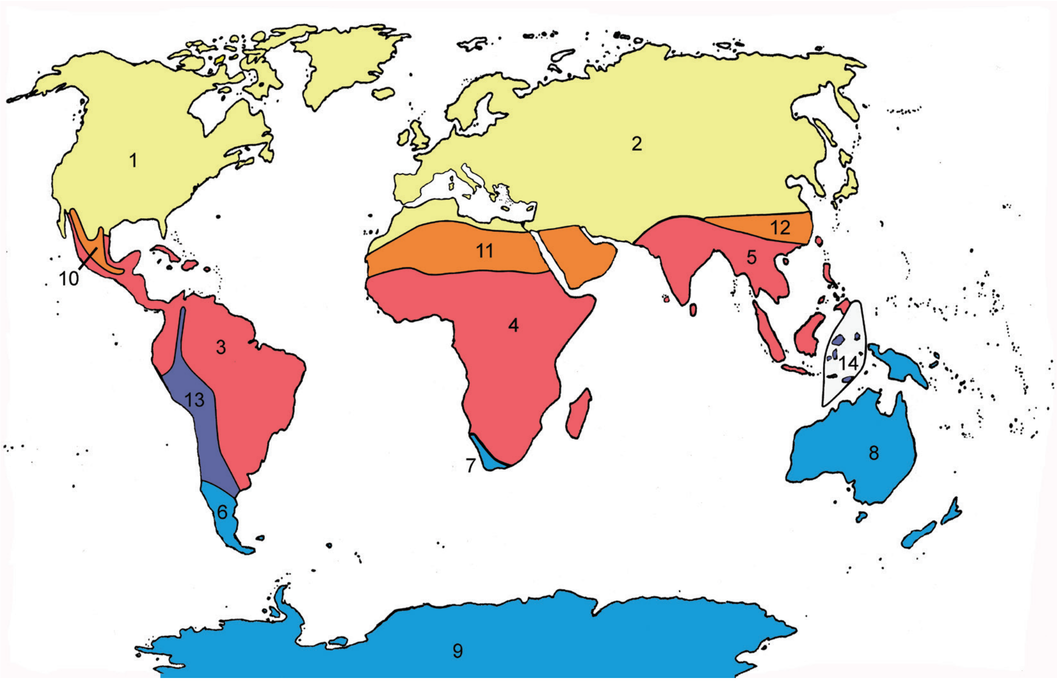

Fig. 2. Biogeographic classification of the Neotropical region in the Holotropical kingdom and identification of transition zones in the overlap with the Nearctic and Anden regions. Color red shows the close relationships between the Neotropics and other regions due to vicariant events. Transition zones represent events of dispersal. 1-2, Holarctic kingdom; 3-5, Holotropical kingdom; 6-9, Austral kingdom; 1, Nearctic region; 2, Palearctic region; 3, Neotropical region; 4, Ethiopian region; 5, Oriental region; 6, Andean region; 7, Cape region; 8, Australian region; 9, Antarctic region; 10, Mexican transition zone; 11, Saharo-Arabian transition zone; 12, Chinese transition zone; 13, South American transition zone; 15, Indomalayan transition zone.

A more precise regionalization and a complete knowledge of the spatial evolutionary history of the mammalian biota of the Neotropics will allow us to propose better strategies for the conservation not only of the biogeographical patterns, but also for maintaining biogeographical processes. Finally, these data also will allow us facing climatic change with better tools.

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