

Conmemoración

A dual biotic nature: What can history tell us about the biogeographical regionalization of Argentina?

Una naturaleza biótica dual: ¿Qué puede decirnos la historia acerca de la regionalización biogeográfica de la Argentina?

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Revista de la Sociedad Entomológica
Argentina vol. 84 núm. 2 e0201 2025

Sociedad Entomológica Argentina
Argentina

Recepción: 11 Febrero 2025

Aprobación: 29 Abril 2025

Abstract: The biogeographic regionalizations of Argentina of different authors, from Wallace (1876) to Arana et al. (2021), are compared and their conceptual frameworks discussed. The existence of a transition zone between the Neotropical and Andean regions is especially analyzed. Currently, six provinces (Yungas, Parana, Araucaria Forest, Chaco, Esteros del Iberá and Pampean) are assigned to the Neotropical region, six provinces (Patagonian, Maule, Valdivian Forest, Magellanic Forest, Magellanic Moorland and Falkland Islands) to the Andean region, and four provinces (Puna, Monte, Cuyan High Andean and Comechingones) to the South American Transition Zone.

Keywords: Andean region, Biogeography, Neotropical region, South American Transition Zone.

Resumen: Se comparan las regionalizaciones biogeográficas de la Argentina de diferentes autores, desde Wallace (1876) hasta Arana et al. (2021) y se discuten sus marcos conceptuales. Se analiza especialmente la existencia de una zona de transición entre las regiones Neotropical y Andina. Actualmente seis provincias (Yungas, Paranaense, Bosque de Araucaria, Chaco, Esteros del Iberá y Pampeana) se asignan a la región Neotropical, seis provincias (Patagónica, Maule, Bosque Valdiviano, Bosque Magallánico, Páramo Magallánico e Islas Malvinas) a la región Andina y cuatro provincias (Puna, Monte, Altoandina Cuyana y Comechingones) a la Zona de Transición Sudamericana.

Palabras clave: Biogeografía, Región Andina, Región Neotropical, Zona de Transición Sudamericana.

INTRODUCTION

Since Wallace's (1876) *The geographical distribution of animals*, evolutionary or historical biogeographers have recognized the dual biogeographic nature of Argentina, with a northern area harboring a tropical biota and a southern area harboring a temperate one. Most of the authors, additionally, have identified a large area of biotic overlap between both areas. This complex pattern has been formally recognized in several biogeographic regionalizations, although the boundaries of the areas and the categories applied to them have varied over the years.

My objectives are to provide a historiographic analysis of Argentina's biotic affinities and to discuss how they have influenced the biogeographic regionalizations of the country. I intend to highlight the relevance of the authors' interpretations of the biogeographic patterns found when studying different taxa, following the path of previous historical analyses (*e.g.*, Willink, 1991; Ribichich, 2002; Lopretto & Menni, 2003; Katinas et al., 2022). I selected some contributions that include regionalization maps, as they provide a visual representation of their proponents's conceptual frameworks (Camerini, 1993).

What could be the relevance of analyzing the biogeographic regionalization of a particular country? Because scientific theories that are exposed to scrutiny from alternative perspectives are more thoroughly tested and, thus, may be more appropriate explanations of the natural world (Oreskes, 2019). The ways different biogeographers have proposed biogeographic regionalizations and how they have represented them on maps show striking similarities, being an interesting subject to analyze. Reviews on the conceptual frameworks of biogeographic regionalizations published in the last decades (*e.g.*, Escalante, 2009; Kreft & Jetz, 2010; Ebach & Parenti, 2015; Morrone, 2018a; Loidi & Vynokurov, 2024) show that their analysis continues exhibiting alternative, and sometimes contradictory, viewpoints.



Figure 1.
Zoogeographic regionalization of the Neotropical region and the subregions recognized by Wallace (1876).

Wallace's *The geographical distribution of animals*

The British naturalist Alfred R. Wallace (1823-1913) made contributions to many areas, notably natural history, geology, evolution, biogeography, astrobiology, spiritualism, and social reform (Smith et al., 2019). Costa (2023) has provided a notable biography of Wallace, highlighting the diverse areas to which he contributed. Wallace's contributions to biogeography are numerous (*e.g.*, Wallace, 1869, 1876, 1880, 1894) and he has been considered the “founder father” of both evolutionary biogeography (Costa, 2019) and conservation biology (Lomolino, 2019). It is interesting that the transition zone between the Oriental and Australian biogeographic regions has been named Wallacea to honor his contributions (Dickerson et al., 1923; Mayr, 1944; Darlington, 1957) and the concept of “Wallacean shortfall” has been articulated by Lomolino (2004) to refer to the insufficient knowledge on the geographical distribution of plants, animals and other organisms of the world.

Wallace's (1876) *The geographical distribution of animals* represents his most important biogeographic contribution. In two volumes, Wallace presented a vast amount of geographical distribution data of animal taxa to characterize the six zoogeographic regions established previously by Sclater (1858), based on bird taxa. Sclater's approach was static, not viewing these regions as a consequence of historical changes (Kinch, 1980). In contrast, Wallace provided an evolutionary explanation for such regions, that promoted the use of regionalizations as organizing principles of biogeographic analyses (Whittaker et al., 2013).

When analyzing the Neotropical region, which Wallace (1876) considered that extended from southern Mexico to southern South America, he established four subregions: Chilean, Brazilian, Mexican, and Antillean (Fig. 1). Most of the Argentinean territory corresponds to the Chilean subregion, whereas the northeastern part of the country corresponds to the Brazilian subregion. Wallace considered that both belonged to the Neotropical region but he treated the Chilean subregion as a transition zone to the Australian region (Wallace, 1876, p. 82).

Wallace's (1876) regionalization of the Neotropical region remained valid for decades, and many zoogeographers used the four subregions when characterizing the biogeographical patterns recognized when studying different animal groups, although they were given alternative names. For example, Wallace's Chilean subregion was renamed Peruvian (Blyth, 1871), Andean-Patagonian (Mello-Leitão, 1937; Ringuelet, 1961; Rapoport 1968; Fittkau, 1969; Hershkovitz, 1969; Sánchez Osés & Pérez-Hernández, 1998), Patagonian (Sclater & Sclater, 1899; Kuschel, 1969), Austral (Ringuelet, 1975), and Argentine (Smith, 1983); and Wallace's Brazilian subregion was renamed Amazonian (Sclater & Sclater,

1899) and Guianan-Brazilian (Mello-Leitão, 1943; Ringuelet, 1961; Rapoport, 1968; Fittkau, 1969).

What is the relevance of Wallace's (1876) contribution? Camerini (1993) has highlighted the importance of Wallace's formulation of a general scheme of biogeographic regions, aimed to unify the different regionalizations that were being discussed in the first half of the nineteenth century, and also his participation in a visual representation that extends into contemporary culture. When people are currently asked about what constitutes biogeography, what immediately comes to many of them are Wallace's biogeographic regions. In fact, some biogeographic regionalizations of the twenty-first century (*e.g.*, Kreft & Jetz, 2010; Procheş & Ramdhani, 2012; Holt et al., 2013; Rueda et al., 2013; Escalante, 2017; Morrone & Ebach, 2022; Falaschi et al., 2023; Liu et al., 2023; Loidi & Vynokurov, 2024) have recognized implicitly or explicitly Wallace's global biogeographic regionalization.

Phytogeographers of the 19th and 20th centuries

During the 19th and 20th centuries phytogeographers and zoogeographers basically kept separate regionalizations (Morrone & Ebach, 2022). In contrast to Wallace (1876), some phytogeographers of the 19th and early 20th century (*e.g.*, Treviranus, 1803; Engler, 1882, 1899) assigned northern and southern South America to different kingdoms (see revision by Moreira-Muñoz, 2007). An interesting author is the German botanist Adolf Engler (1844-1930), who described the Old Ocean kingdom, uniting southern Chile and New Zealand's South Island (Engler, 1882). Engler's (1882) map (Fig. 2) shows the boundaries of the Old Ocean kingdom, later renamed Austral kingdom (Engler, 1899), and the South American kingdom in southern Chile, where all the Argentinean territory belongs to the latter. Both Drude (1884) and Diels (1908) separated southern South America and New Zealand into independent kingdoms.

In the 20th century, phytogeographers mostly followed Engler's proposals, although some of them tried to accommodate them to Wallace's regionalization (*e.g.*, Arltdt, 1907). The phytogeographic schemes of Good (1947) and Takhtajan (1961, 1986), widely used during the second half of the 20th century, continued recognizing both kingdoms, although these authors renamed the Austral kingdom to Antarctic and Holarctic, respectively. The relevance of these phytogeographic regionalizations has been clearly shown by Moreira-Muñoz (2007), who reviewed them especially focusing on the Austral kingdom, and concluded that its recognition was well-supported by 60 genera and 15 plant families of angiosperms.

Ángel Cabrera's Argentinean phytogeography

Ángel L. Cabrera (1908-1999) was a Spanish-Argentinean botanist and phytogeographer, who made the most important contributions

to the phytogeographic regionalization of the country (Cabrera, 1951, 1953, 1957, 1958, 1971, 1976; see Katinas et al., 2022). *Esquema fitogeográfico de la República Argentina* (Cabrera, 1953) presented a detailed historical review and some general methodological remarks. In this contribution, Cabrera reproduced some previous regionalization maps based on the vegetation of the country (*e.g.*, Lorentz, 1876; Holmberg, 1898; Rovereto, 1914; Hauman, 1920, 1931; Kühn, 1930; Parodi, 1934, 1945; Castellanos & Pérez-Moreau, 1941, 1944), and presented a map with his phytogeographic scheme, that differs slightly from two maps published later by him (Cabrera, 1971, 1976).

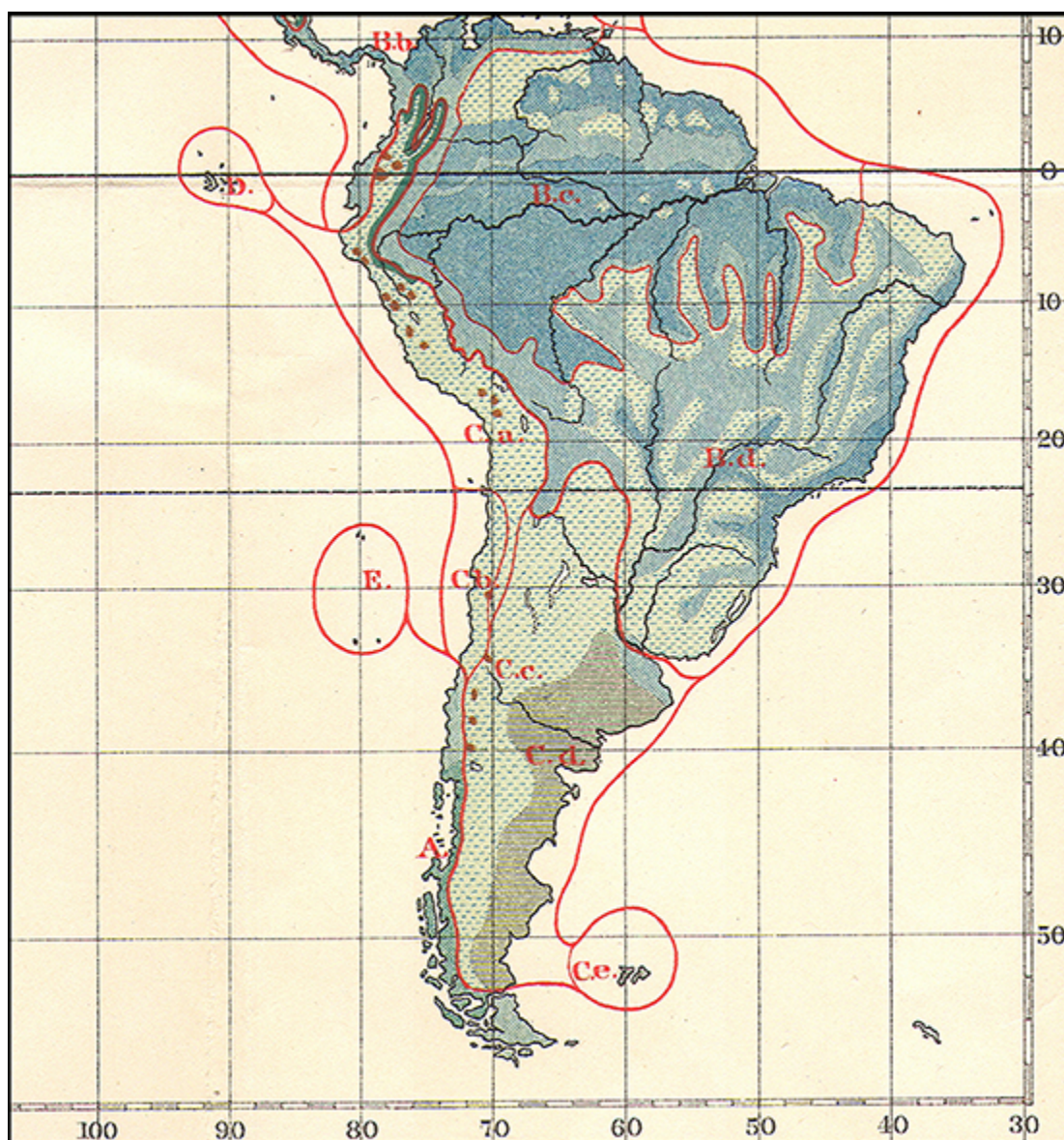


Figure 2.

Phytogeographic regionalization of South America according to Engler (1882), showing the boundaries of the Old Ocean and South American kingdoms in southern Chile.

References= A.: Old Ocean kingdom, B: Tropical American region, B.b: Subandean province, B.c: North Brazilian-Guyanese province B.d: South Brazilian province, C.a: Northern High Andean province, C.b: North Chilean province, C.c: Argentinean-Patagonian province, C.d: Pampas province, C.e: Falkland islands province, D: Galapagos Islands region, E: Juan Fernández region.

Fitogeografía de la República Argentina (Cabrera, 1971) and *Regiones fitogeográficas argentinas* (Cabrera, 1976) are the most complete presentations of Cabrera's regionalization of the country. I find Cabrera's (1976) contribution particularly clear, with the names previously given to the areas and data on relief, soil, climate, vegetation, and species characteristic of each plant community. Cabrera's phytogeographic scheme of Argentina (Fig. 3) is as follows:

Neotropical region
 Amazonian dominion
 Yunga province
 Transition Forests district
 Mountain Forests district
 Mountain Woods district
 Paranense province
 Mixed Forests district
 Campos district
 Chacoan dominion
 Chacoan province
 Eastern Chacoan district
 Western Chacoan district
 Mountainous Chacoan district
 Sabanas district
 Espinal province
 Nandubay district
 Algarrobo district
 Caldén district
 Prepunan province
 Monte province
 Pampean province
 Uruguayan district
 Eastern Pampean district
 Western Pampean district
 Austral Pampean district
 Andean-Patagonian dominion
 High Andean province
 Quichua High Andean district
 Cuyan High Andean district
 Austral High Andean district
 Punan province
 Patagonian province
 Payunia district
 Western Patagonian district
 Central Patagonian district
 San Jorge Gulf district
 Subandean Patagonian district
 Fuegian district
 Antarctic region
 Subantarctic dominion
 Subantarctic province
 Pehuén district
 Deciduous Forest district
 Valdivian district
 Magellanic district
 Insular province
 Antarctic dominion
 Antarctic province

The treatment given by Cabrera to the dual biotic affinities of Argentina followed Engler (1899) and Mattick (1964), although he categorized these areas as phytogeographic regions: Neotropical and Antarctic. Most of the Argentinean continental territory corresponds to the Neotropical region, and only a narrow strip along the eastern Andean slope and the South Atlantic islands were assigned to the Antarctic region. Cabrera's phytogeographic regionalization has been followed by most of the botanists from Argentina and also by governmental and non-governmental organizations dealing with the conservation of the flora (Ribichich, 2002).

Cabrera contrasted ecological (physiognomic, phytosociological and dynamic) and historical (floristic) phytogeographic regionalizations, choosing the latter as the most appropriate (Katinas et al., 2022). Cabrera's basic theoretical assumptions are as follows:

(1) the spatial distribution of a species in a primary center of dispersal is coincident with its center of origin; (2) the distributional area of a species is increased by dispersal and successful establishment; (3) the distributional areas of different species are coincident as they have similar ecological requirements and evolutionary history; (4) some geographical features are of great relevance, constituting either dispersal routes or barriers; (5) climatic factors are the most relevant in the distribution of plants; (6) plant communities changer over time, eventually achieving a stable state, named climax community; (7) climax plant associations may be grouped based on their phylogenetic relationships; and (8) phytogeographic areas are real territories whose boundaries are determined by climatic, edaphic and geological factors (Ribichich, 2002).

Ribichich (2002) reviewed Cabrera's regionalization, concluding that it has some problematic issues and should not be applied indiscriminately for biogeographic analyses. She noted especially the absence of justifications and methodological details, following a narrative style common to traditional phytogeographers, and also some contradictory statements between the suggested affinities and the classification of the areas. Despite her criticisms, Ribichich's (2002) concluded highlighting the relevance of Cabrera's regionalization as a hypothesis, subject to criticism and revision.

Katinas et al. (2022) reviewed the phytogeographic regionalizations of Frenguelli (1940) and Cabrera (1953, 1971; Cabrera & Willink, 1973), based on vegetation and floristics, respectively. The historical approach of Cabrera, according to Katinas et al. (2022), resulted to be the most successful in posterior regionalizations, even in those considering animal taxa (*e.g.*, Morrone, 2014, 2015), that are more similar to Cabrera's scheme than to Ringuet's (1961).

Raúl Ringuet's zoogeographic contributions

Raúl A. Ringuet (1914-1982) was an Argentinean zoologist, ecologist, limnologist and biogeographer, that produced a vast number of publications in different animal taxa (see Schnack, 1982; Menni, 1983). His biogeographic contributions refer to many distinct subjects (compiled by López & Ponte Gómez, 2015), being especially relevant those dealing with Neotropical Hirudinea (Ringuet, 1944, 1978), Argentinean scorpions (Ringuet, 1953), the Subantarctic dominion (Ringuet, 1955a, b), Opiliones (Ringuet, 1957, 1959), Argentinean zoogeography (Ringuet, 1961), copepods (Ringuet, 1968), and freshwater biogeography of South America (Ringuet, 1975). Lopretto & Menni (2003) have provided an exhaustive analysis of Ringuet's biogeographic contributions, highlighting his integrative treatment of both ecological and historical factors.

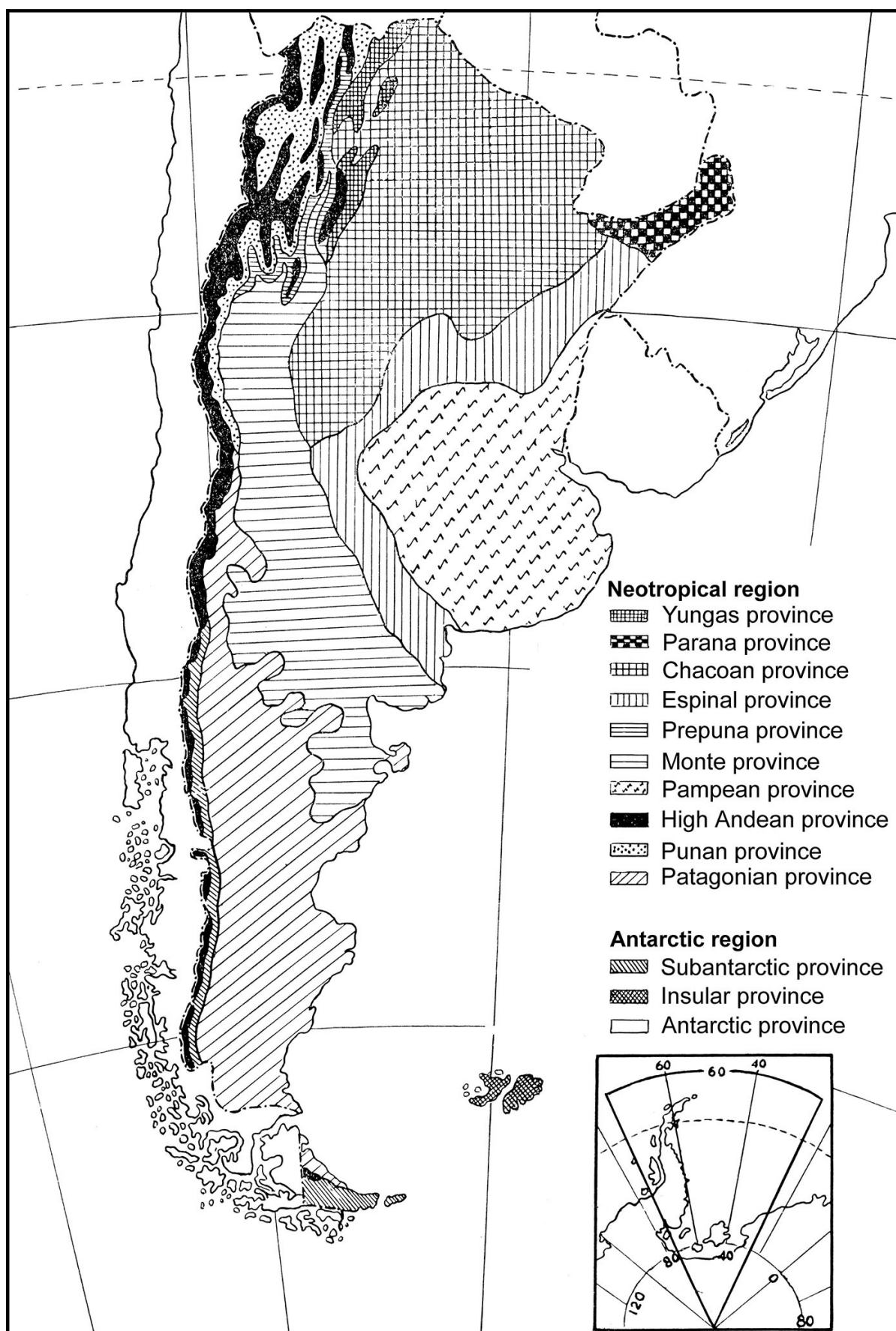


Figure 3. Cabrera's (1971) phytogeographic map of Argentina.

Rasgos fundamentales de la zoogeografía de Argentina (Ringuelet, 1961) is Ringuelet's most important and synthetic treatment of the general zoogeography of the country (Lopretto & Menni, 2003). There he discussed some conceptual issues, emphasizing that both ecological and historical aspects should be considered when analyzing the biogeography of an area. Ringuelet (1961) characterized six distributional types in the fauna of the country: (1) Gondwanic (Neotropics, South Africa and the Australian region); (2) Austral or Notogaic (Neotropics and the Australian region); (3) Amphiatlantic (South America and Africa); (4) Andean; (5) disjunct in the Pampean hills; and (6) continuous due to uniform ecological conditions. The basic features of the zoogeography of Argentina identified by Ringuelet (1961) are the following: (1) each area recognized within the country has a particular fauna with different biotic origins ("estirpes") but ecologically similar; (2) there is a general congruence between the distribution of the Brazilian or Guianan-Brazilian fauna and the areas related to the Brazilian craton; (3) the southwards dispersal of the Brazilian fauna has exceeded its current boundaries in pre-Quaternary times; (4) there is general congruence between the distribution of notogaic animal taxa with the Andean-Patagonian and Araucanian subregions; (5) there is a clear distinction between the forest fauna of the Guianan-Brazilian subregion, the xeric fauna of the Andean-Patagonian subregion, and the mountain fauna of the Araucanian subregion; (6) there has been an ecological dynamism in the secular boundaries of the Guianan-Brazilian and the Andean-Patagonian faunas; (7) there is no congruence between the current hydrography and the zoogeography of freshwater animals; (8) faunistic "islands" and other isolated areas indicate dispersal from other areas and changes in ecological conditions; (9) the Pampean hills exhibit faunistic disjunctions; and (10) the Río de la Plata has served as a colonization route of freshwater species from the Atlantic Ocean.

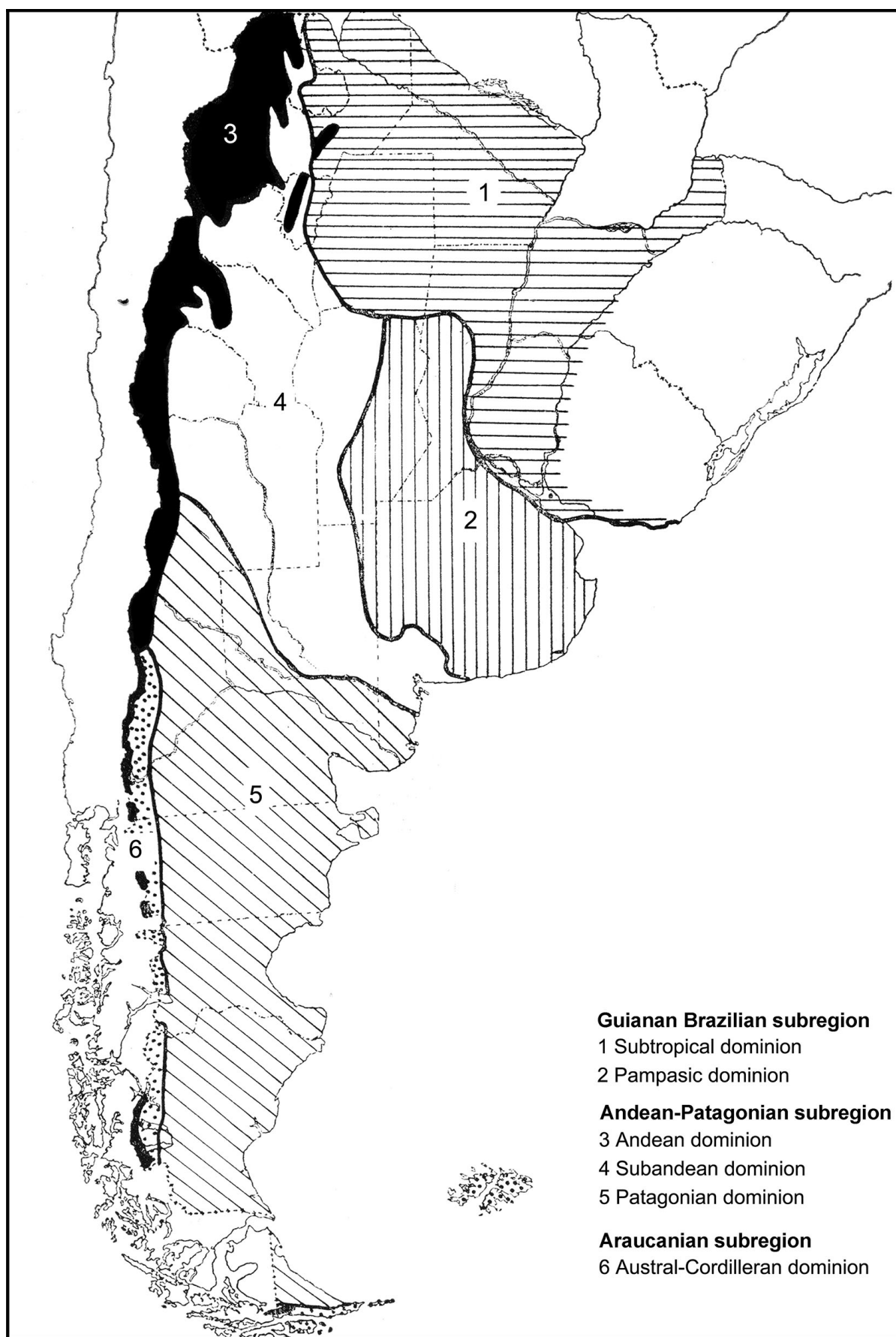


Figure 4.

Zoogeographic regionalization of Argentina according to Ringelet (1961).

The zoogeographical scheme of Argentina presented by Ringelet (Fig. 4) is as follows:

Neotropical region
 Guianan-Brazilian subregion
 Subtropical dominion
 Misiones district
 Chacoan district
 Tucumán-Salta district
 Mesopotamic district
 Pampasic dominion
 Andean-Patagonian subregion
 Andean dominion
 Southeastern district
 Patagonian dominion
 Central or Subandean dominion
 Subandean district
 Araucanian subregion
 Austral-Cordilleran dominion
 Continental district
 Malvinas district

In contrast to Cabrera, Ringelet (1961) assigned Argentina (and all South America) to the Neotropical region, as did Wallace (1876). Concerning the subregions that correspond to the country, however, Ringelet (1961) distinguished three subregions instead of two, and subdivided them into six dominions and seven districts. A similar phytogeographic regionalization of the Neotropical kingdom was proposed by Rivas-Martínez & Tovar (1983), recognized four subkingdoms: Caribbeo-Amazonian, Chacoan, Andean (= Ringelet's Andean-Patagonian subregion), and Subantarctic (= Ringelet's Araucanian subregion).

Ringelet's (1961) regionalization has been the basic zoogeographic scheme of Argentina for half a century (Lopretto & Menni, 2003). For example, when Maury (1979) analyzed the geographic distribution of Argentinean scorpions, he compared his results with those of Ringelet (1961).

Kuschel's Problems concerning an Austral region

Guillermo Kuschel (1918-2017) was a Chilean-New Zealander entomologist, who made some contributions to the zooogeography of southern South America (e.g., Kuschel, 1960, 1961, 1962, 1964, 1969). In 1961 Kuschel participated in a symposium on Pacific Basin biogeography, that was organized in the Tenth Pacific Science Congress, Honolulu, Hawaii (Gressitt et al., 1964).

Kuschel's (1964) *Problems concerning an Austral region* explored the possibility of recognizing a region encompassing Australia, New Guinea, New Zealand, southern South America, South Africa, Antarctica, and the Subantarctic islands (Fig. 5). Kuschel considered

that there was enough evidence to place southern South America or Patagonia with Australasia and other southern areas instead of treating it as part of the Neotropical region. He found that in addition to its truly Patagonian (xeric) and Neotropical elements, southern South America had an Austral faunistic element common to the other southern continents, stating that the reasons for combining the Patagonian and Australian subregions were as strong as those for combining the Nearctic and Palearctic regions. Kuschel (1964) hypothesized that the overlap between Patagonian and Neotropical elements was quite large, because open country elements could disperse quite easily northwards and southwards in the past, with some Patagonian taxa currently reaching southern Brazil, Paraguay, and Bolivia, and some Neotropical taxa currently found right down to Tierra del Fuego. Based on his knowledge of weevils (Coleoptera: Curculionidae) he would assign the Patagonian subregion to the Austral region, but he cautiously considered that such a decision would need to be based on many different taxa.

Assigning southern South America to the Austral kingdom and northern South America to the Holotropical kingdom has been supported by posterior studies. Crisci et al. (1991) and Amorim & Tozoni (1994) are examples of cladistic biogeographic analyses showing that each of these regions is related to different areas of the world. Moreira-Muñoz (2007) and Morrone (2015, 2018b) also supported the separation of an Austral kingdom. Carta et al.'s (2022) phylogenetic regionalization based on vascular plants of the world found a clear separation between Australia-New Zealand-Patagonia and the tropical areas of the world, supporting splitting South America into different regions and kingdoms.

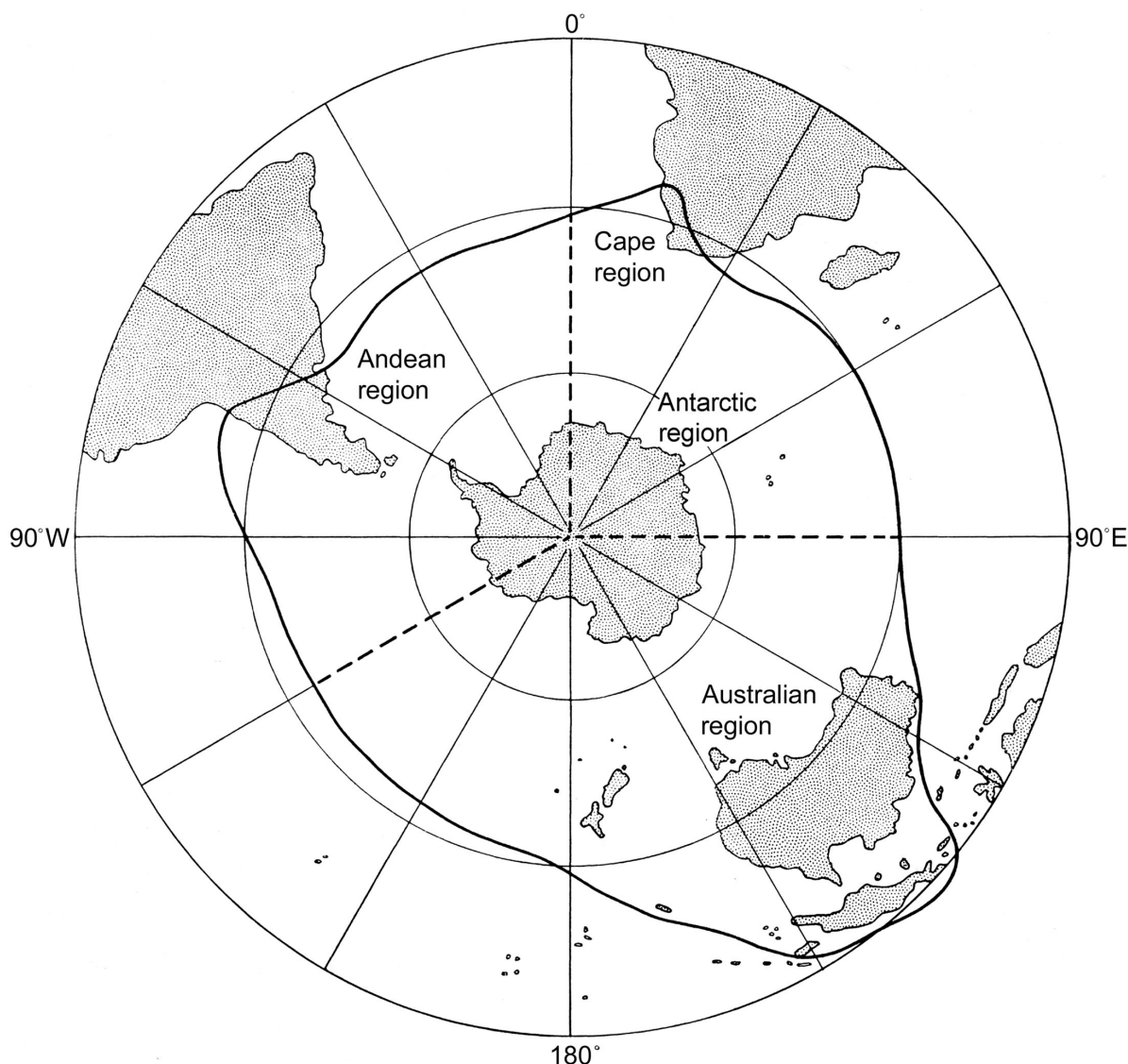


Figure 5.
Austral region as proposed by Kuschel (1964).

Rapoport's "subtropical line"

Eduardo H. Rapoport (1927-2017) was an Argentinean ecologist and biogeographer, who made relevant contributions to macroecology and ecological biogeography (Ruggiero, 2005). His chapter in *Biologie de l'Amerique Australe* (Delamare Deboutville & Rapoport, 1968) constitutes a general review of the biogeographic regionalization of the Americas, with some conceptual discussions.

Algunos problemas biogeográficos del Nuevo Mundo con especial referencia a la región Neotropical (Rapoport, 1968) compiled some zoogeographic regionalizations of South America, proposed a general regionalization of the world and discussed the relationships of the Neotropics with other regions. Rapoport (1968) discussed previous zoogeographic maps and discussed their differences and similarities,

concluding that the Neotropical region should be divided into the Central American, Antillean, Guianan-Brazilian, Andean-Patagonian, and Araucanian subregions, providing examples of taxa endemic to them. He justified the recognition of the Araucanian subregion, based on the work of Monrós (1958) and other authors, which he found was especially valid for invertebrates. Then, Rapoport (1968) discussed the existence of a “subtropical line” separating the Guianan-Brazilian and Andean-Patagonian subregions (Fig. 6) as delineated by Sclater (1858), Wallace (1876), Mello-Leitão (1937), and Ringuelet (1955c, 1961). Rapoport (1968) provided several examples, showing how this line varies according to the taxa analyzed.

Rapoport (1968) also presented a new regionalization of the world, recognizing three biogeographic regions: Holarctic, Holotropical, and Holantarctic. Each of these regions corresponds to a latitudinal “belt” delimited approximately by the Tropics of Cancer and Capricorn. Most of the Argentinean territory (Neotropics) belongs to the Holotropical region, whereas a small portion (Araucanian) was assigned by Rapoport to the Holantarctic region, which is coincident with Kuschel’s (1964) Austral region. Rapoport provided several examples of taxa showing biotic connections of South America either with tropical (Holotropical) and temperate (Holarctic and Holantarctic) areas.

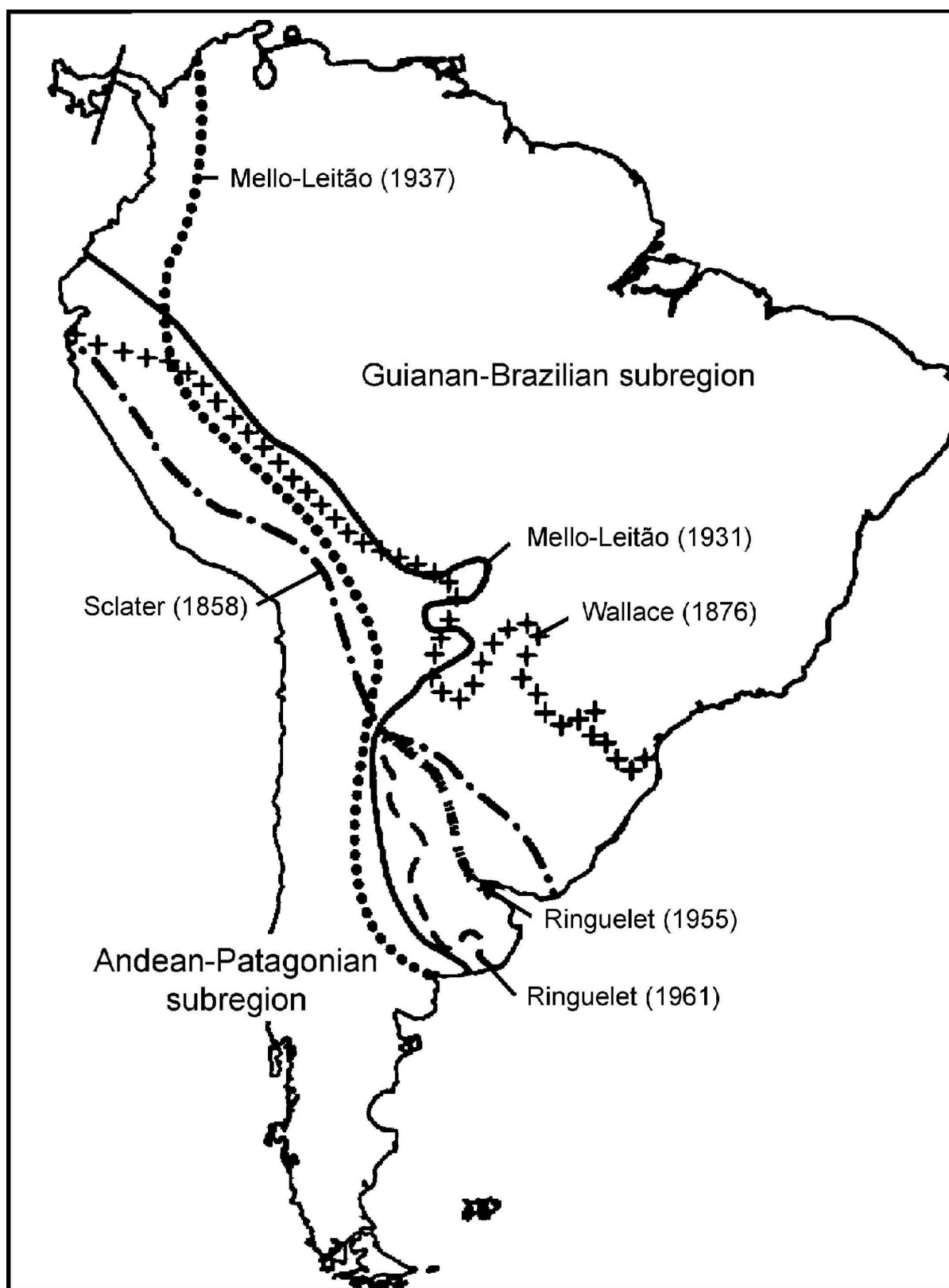


Figure 6.

Alternative placements of the “subtropical line” separating the Guianan-Brazilian and Andean-Patagonian subregions analyzed by Rapoport (1968).

Cabrera & Willink's (1973) Biogeografía de América Latina

In 1973, Ángel L. Cabrera joined the Dutch-Argentinean entomologist Abraham Willink (1920-1998) to publish a biogeographic regionalization of the Americas south of the United States. Willink has made several contributions to the systematics and biogeography, but Cabrera & Willink's (1973) monograph is the one that had the biggest impact (Claps et al., 2013).

Biogeografía de América Latina (Cabrera & Willink, 1973) considers both plant and animal taxa. The authors present six short chapters dealing with historical and conceptual issues, *e.g.*, distributional areas, biocenoses and ecosystems, plant biological types, vegetation, and the phytogeographic and zoogeographic regions of the world. The Latin American areas were assigned to the Holarctic, Neotropical, Antarctic, and Oceanic regions, and within them 12 dominions and 31 provinces. The Argentinean territory was divided into nine provinces, assigned to the Neotropical and Antarctic regions, basically following Cabrera (1953, 1971).

Willink (1991) reviewed several zoogeographic contributions to the study of Argentinean insects and discussed their faunistic relationships. When dealing with the regionalization of the country, Willink represented the portion of the map (Fig. 7) according to Cabrera & Willink (1973).

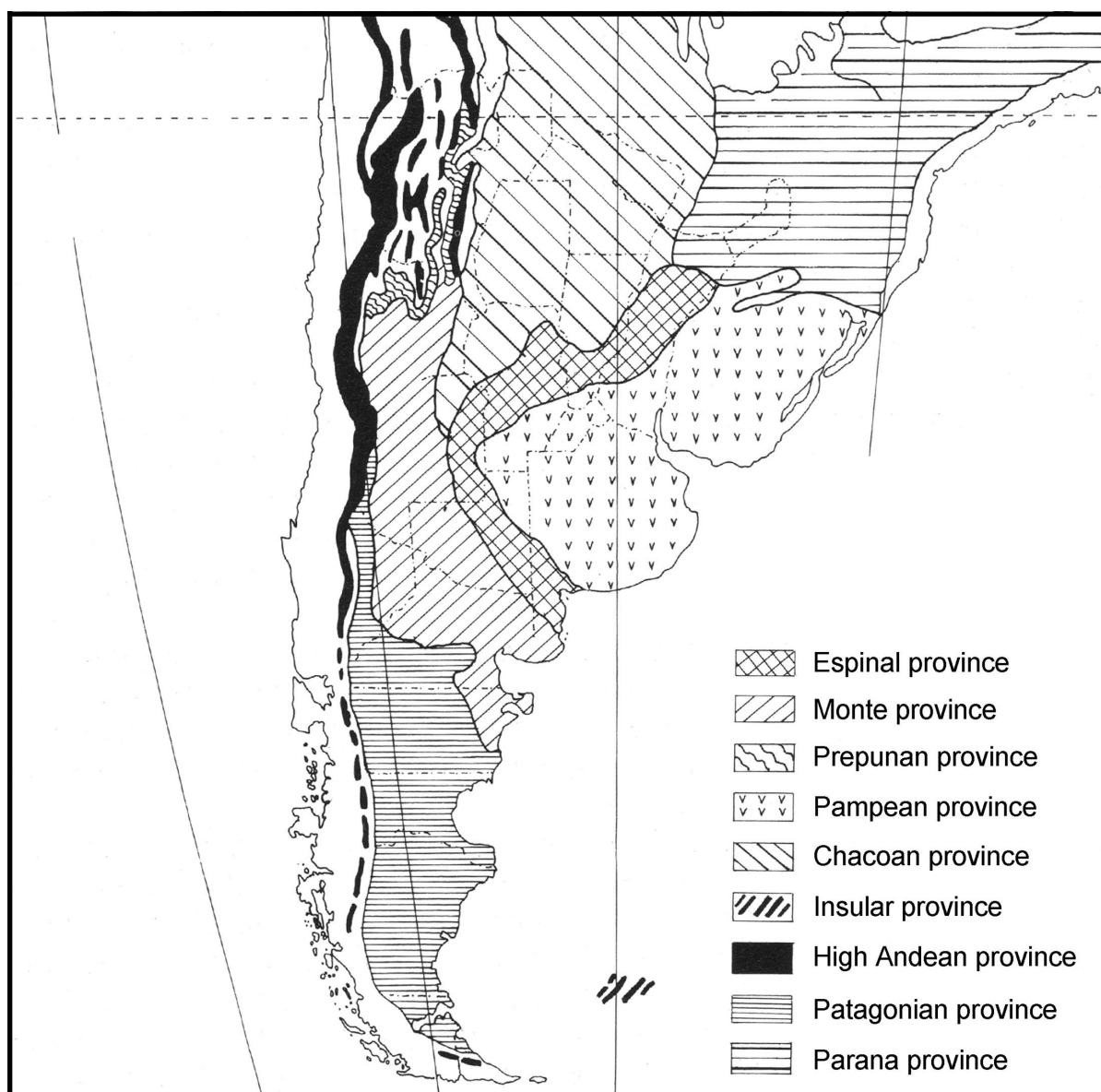


Figure 7.
Biogeographic regionalization of Argentina according to Willink (1991).

Arana et al.'s (2021) Esquema biogeográfico de la República Argentina

Arana et al. (2017, 2021) provided the most recent biogeographic regionalization of the country, following the biogeographic regionalizations of Morrone (2014, 2015, 2017, 2018b). Two previous contributions (Morrone, 2001, 2006) were based on plant and animal taxa, where insects played a relevant role in characterizing the regions, subregions, dominions, and provinces. The biogeographic provinces of Argentina were assigned by Arana et al. (2017, 2021) to the Neotropical and Andean regions, and four provinces as part of both regions, belonging to the South American Transition Zone. When delimiting the provinces and districts within each province,

the presence of endemic species was the basic criterion, but the ecoregions of Olson et al. (2001) were used to delineate their boundaries on the maps.

The regionalization of *Esquema biogeográfico de la República Argentina* (Fig. 8; for maps of the districts recognized within each province, see Arana et al., 2021) is as follows:

Holotropical kingdom
 Neotropical region
 Brazilian subregion
 South Brazilian dominion
 Yungas province
 Mountain Forests district
 Mountain Jungles ("Selvas") district
 Transition Forests district
 Chacoan subregion
 Parana dominion
 Parana province
 Campos district
 Mixed Forests district
 Esteros del Iberá province
 Parana Flooded Savannas district
 Uruguay River district
 Parana Delta district
 Araucaria Forest province
 Chacoan dominion
 Chaco province
 Western Chacoan district
 Eastern Chacoan district
 Mountainous ("Serrano") Chacoan district
 Pampean province
 Uruguayan district
 Espinal district
 Eastern Pampean district
 Western Pampean district
 Austral Pampean district
 South American Transition Zone
 Puna province
 Jujuyan district
 Cuyan High Andean province
 Diaguita district
 Cuyan district
 Huarpe district
 Monte province
 Prepunan district
 Northern district
 Eremian district
 Austral district
 Comechingones province
 Austral kingdom
 Andean region
 Patagonian subregion
 Patagonian province
 Payunia subprovince
 Northern Payunia district
 Austral Payunia district
 Subandean subprovince
 Austral High Andean district
 Northern Subandean Patagonia district
 Southern Subandean Patagonia district
 Western Patagonian subprovince
 Central Patagonian subprovince
 Chubut district
 Santa Cruz district
 Fuegian subprovince
 Subantarctic subregion
 Maule province
 Pehuén district
 Valdivian Forest province
 Valdivian district
 Magellanic Forest province
 Falkland Islands province
 Falkland Islands district
 South Georgia Islands district
 Magellanic Moorland province

Arana et al.'s (2021) biogeographic regionalization recognizes the basic division between the Neotropical region, that is assigned to the Holotropical kingdom, and the Andean region, that is assigned to the Austral kingdom (Morrone & Ebach, 2022). In addition, the Puna, Monte, Cuyan High Andean and Comechingones provinces are assigned to the South American Transition Zone, to highlight their dual Neotropical-Andean connections.

This biogeographic regionalization is the first to recognize formally the South American Transition Zone and the dual nature of the Puna, Monte, High Andean and Comechingones provinces, which were treated by the previous authors as part of the Neotropical region. A recent contribution by Roig-Juñent et al. (2018) has postulated that the Patagonian province should also be assigned to the South American Transition Zone, instead of being part of the Andean region in the strict sense.

DISCUSSION

Biogeographic regionalizations are general reference systems that allow communication among biogeographers, macroecologists, systematists, evolutionary biologists and conservationists (Morrone, 2018a). The biogeographic regionalization of Argentina has evolved for a century and a half, beginning with Wallace's (1876) map of the subregions of the Neotropical region, passing through contributions by Cabrera, Ringuet, Kuschel, and Rapoport, among others, to finally arrive to Arana et al.'s (2021) scheme of regions, subregions, dominions, provinces, and districts. The dual biogeographic nature of Argentina has been dealt in most of the regionalizations analyzed, since Wallace (1876) to most recent analyses (*e.g.*, Carta et al., 2022; Falaschi et al., 2023; Liu et al., 2023; Loidi & Vynokurov, 2024).

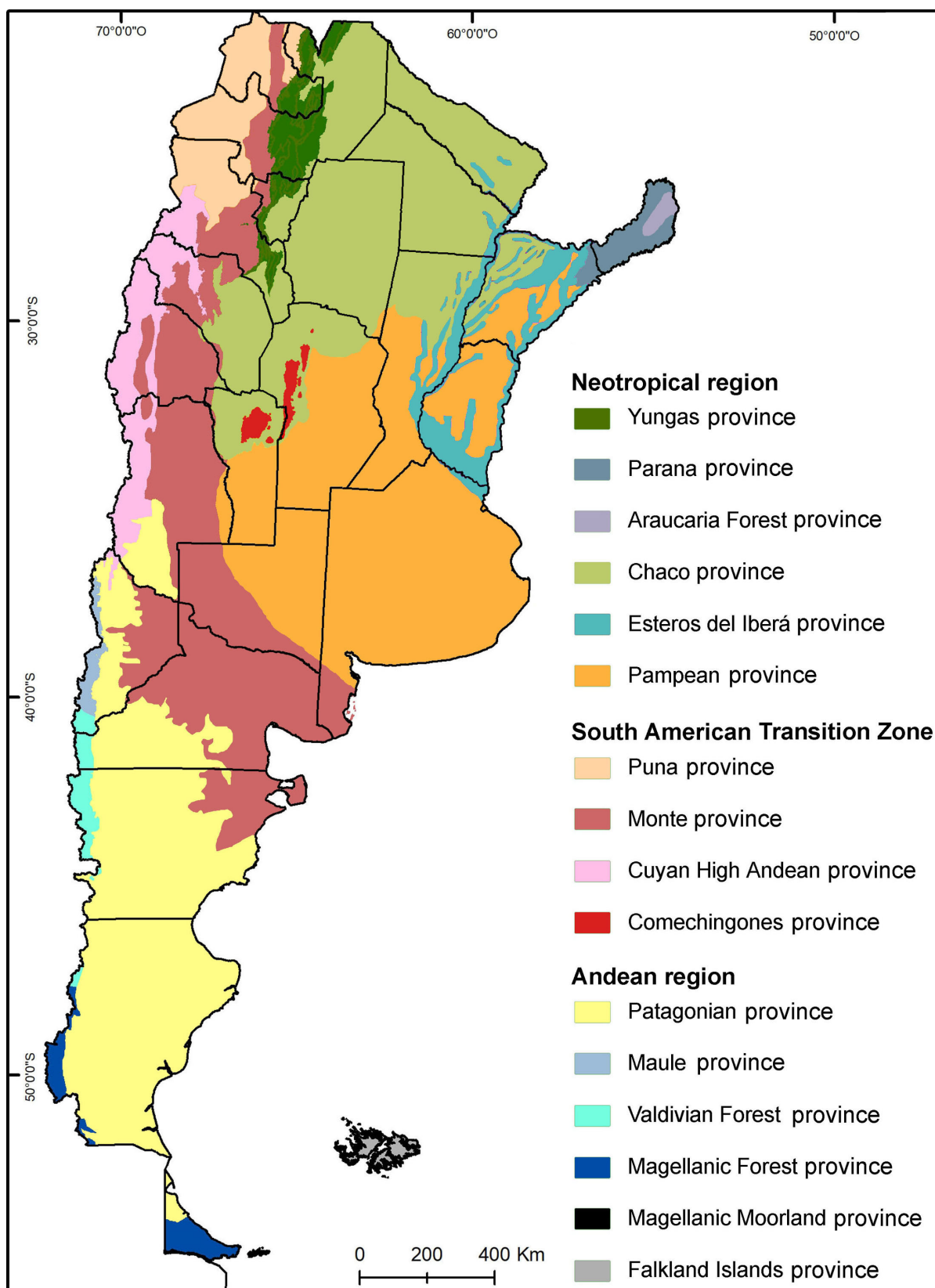


Figure 8.
Biogeographic regionalization of Argentina according to Arana et al. (2021).

Whether southern and northern South America are assigned to different regions or kingdoms, or whether a transition is recognized in their overlap, however, differs greatly and depends on the taxa analyzed and the methods used. It is interesting that insect taxa have provided relevant data for the identification of areas of endemism and for assessing their biotic relationships (*e.g.*, Ringuelet, 1955a, b; Monrós, 1958; Kuschel, 1969; Amorim & Tozoni, 1994; Morrone, 2001, 2006; Roig-Juñent et al., 2018). Future studies incorporating distributional and phylogenetic information may test the current biogeographic regionalization, modifying the extension of the regions and the transition zone or allowing the description of new provinces and districts. Furthermore, exploring insect distributional patterns with new analytical techniques (*e.g.*, Carta et al., 2022; Gross et al., 2025) may provide new insights to the biogeographic regionalization of Argentina.

In contrast to the evolutionary or historical regionalizations based on endemic taxa, ecoregions have also been recognized (*e.g.*, Burkart et al., 1999; Olson et al., 2001; Morello et al., 2018). Olson et al. (2001) produced a general ecoregionalization of the world, where ecoregions correspond to sizable units encompassing distinct assemblages of communities and species, delineated by boundaries aligned to the historical extent of natural habitats before significant land-use alterations occurred. There are many instances where ecogeographic and evolutionary regionalizations are coincident, as biotas are molded by both historical and ecological factors (Arana et al., 2017, 2021; Morrone et al., 2022). If we contrast Arana et al.'s (2021) regionalization with the most recent ecoregional regionalization of the country (Morello et al., 2018), some of the provinces and districts recognized are equivalent to the ecoregions and to the smaller units recognized within them. This clearly shows the relevance that future studies will have in the establishment of an integrative biogeographic general reference system for the country. I hope this contribution will spark interest in this endeavor!

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**A dual biotic nature: What can history tell us about the
biogeographical regionalization of Argentina?**

**Una naturaleza biótica dual: ¿Qué puede decirnos la historia
acerca de la regionalización biogeográfica de la Argentina?**

Revista de la Sociedad Entomológica Argentina

vol. 84, núm. 2, e0201, 2025

Sociedad Entomológica Argentina, Argentina

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ISSN-E: 1851-7471



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