

Biogeographical regionalisation of the world: a reappraisal

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Abstract. Some phytogeographical, zoogeographical and biogeographical regionalisations of the world are reviewed qualitatively. A biogeographical regionalisation attempting some consensus is proposed, recognising the following three kingdoms and nine regions: Holarctic kingdom (Nearctic and Palearctic regions), Holotropical kingdom (Neotropical, Ethiopian and Oriental regions) and Austral kingdom (Cape, Andean, Australian and Antarctic regions). Additionally, the following five transition zones are recognised: Mexican (Nearctic–Neotropical transition), Saharo-Arabian (Palearctic–Ethiopian transition), Chinese (Palearctic–Oriental transition), Indo-Malayan (Oriental–Australian transition) and South American (Neotropical–Andean transition).

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Introduction

The biogeographical regionalisation of the world has been a relevant area of research during the past two centuries. After the initial efforts of Sclater (1858), Wallace (1876) and Engler (1879, 1882), among others, several biogeographical regionalisations have been proposed. In spite of basic disagreements between those regionalisations proposed by phytogeographers and those by zoogeographers (Cox 2001), there have been some efforts to provide unified schemes (Udvardy 1975; Pielou 1979, 1992; Müller 1986; Morrone 2002). In recent years, biogeographical regionalisation has received a renewed interest (Escalante 2009; Whittaker *et al.* 2013; Vilhena and Antonelli 2014), with the development of specific methodologies and the analysis of large databases (Procheş 2005; Kreft and Jetz 2010; Procheş and Ramdhani 2012; Holt *et al.* 2013a; Rueda *et al.* 2013; Ribeiro *et al.* 2014). These efforts have provided new insights and also shown some conflicts with previously proposed regionalisations. Kreft and Jetz (2013) provided a methodological critique of Holt *et al.* (2013a), warning that biogeographers should be aware of the limitations of providing arbitrary boundaries, because of the existence of transition zones between the regions. They especially criticised the proposal of the Saharo-Arabian, Sino-Japanese and Panamanian new kingdoms, considering that they merely represented some of the transition zones previously recognised by other authors (e.g. Müller 1986).

My objectives are to review previous regionalisations and to present a revised biogeographical regionalisation that explicitly recognises transition zones between the regions. This regionalisation is intended to represent a working hypothesis, from which specific statements on patterns and processes can be deduced and falsified with distributional and phylogenetic data of plant and animal taxa. This contribution does

not represent a quantitative analysis, but is an attempt of reaching some consensus between previous proposals. I hope it will encourage authors analysing different taxonomic groups to falsify this biogeographical scheme.

On biogeographical regionalisation

A biogeographical regionalisation is a hierarchical system that categorises geographical areas in terms of their biotas (Ebach *et al.* 2008; Escalante 2009). During the past two centuries, several biogeographical regionalisations have been proposed for the world and for particular areas. Initially, they were done intuitively, although as early as 1820, de Candolle proposed that kingdoms should harbour a minimum of endemic species and genera so as to be accepted (de Candolle 1820). Wallace (1876) discussed some principles that should be applied for obtaining natural regionalisations (Rueda *et al.* 2013). Drude (1884) postulated that phytogeographic kingdoms should be based on endemic families. The past decades have witnessed efforts for producing biogeographical regionalisations in a more objective way, although there is little agreement on the use of different methods, such as, for example, similarity measures, species turnover, track analyses, parsimony analysis of endemism, cladistic biogeography, phylogenetic similarity, provinciality and higher-order presence-absence patterns (Kreft and Jetz 2010; Krivokhatsky and Ovtshinnikova 2012; Procheş and Ramdhani 2012; Holt *et al.* 2013a; Vilhena and Antonelli 2014). Some authors consider that to produce natural biogeographical regionalisations, successively nested endemism should be the only criterion used (Morrone 2008; Escalante 2009), as has been the case traditionally (e.g. Sclater 1858; Wallace 1876; Engler 1879).

Biogeographical regionalisation is historically rooted in the 19th century, with classificatory and nomenclatural procedures

similar to those of systematics (Morrone 2009; Parenti and Ebach 2009). After recognising natural areas based on endemic taxa, they need to be arranged hierarchically and given names. So as to denote this hierarchy, the following five basic hierarchical levels are used: kingdoms (also known as realms), regions, dominions, provinces and districts; in some cases, subkingdoms, subregions or subprovinces are recognised. In the present contribution, I used the kingdom and region levels. So as to deal with the already proposed names, I followed the nomenclatural conventions set out in the International Code of Area Nomenclature or ICAN (Ebach *et al.* 2008), applying the notion of priority for using older names instead of new ones. Sclater (1858) was adopted as the date of the starting point of biogeographical nomenclature, because it constitutes the first widely adopted world biogeographical regionalisation (Morrone 2014). In addition to the kingdoms and regions, I considered transition zones, which represent areas of overlap, with a gradient of replacement and partial segregation between the biotas belonging to different regions (Ferro and Morrone 2014). Although transition zones have been discussed by several authors (Schmidt 1954; Darlington 1957; Müller 1986; Palestini and Zunino 1986; Ruggiero and Ezcurra 2003; Procheş 2005; Riddle and Hafner 2010), their incorporation to a formal regionalisation of the world has been uncommon.

Historical account

Sclater (1858) divided the world into six zoogeographical regions, based on bird taxa. These regions are as follows: Palearctic, Ethiopian or Western Paleotropical, Indian or Middle Paleotropical, Australian or Eastern Paleotropical, Nearctic or North American and Neotropical or South American. He grouped the Nearctic and Neotropical regions in the Neogean creation and the Palearctic, Ethiopian, Indian and Australian regions in the Paleogean creation. A few years later, Wallace (1876) accepted Sclater's (1858) regional scheme and applied it to other vertebrate taxa, promoting its use as an organising principle of biogeography (Whittaker *et al.* 2013). Within each region, Wallace (1876) recognised four subregions, considering that some of them were transitional between two regions: Mediterranean (Palearctic–Ethiopian transition), Siberia (Palearctic–Nearctic transition), Manchuria (Palearctic–Oriental transition), East Africa (Ethiopian–Palearctic transition), Hindostan (Oriental–Ethiopian transition), Indo-China (Oriental–Palearctic transition), Indo-Malaya (Oriental–Australian transition), Austro-Malaya (Australian–Oriental transition), New Zealand (Australian–Neotropical transition), Chile (Neotropical–Australian transition), Mexico (Neotropical–Nearctic transition), Rocky Mountains (Nearctic–Neotropical transition) and Canada (Nearctic–Palearctic transition).

The Sclater–Wallace system was followed by many zoogeographers (e.g. Murray 1866; Huxley 1868; Kirby 1872; Allen 1892; Sclater 1894; Heilprin 1887; Bartholomew *et al.* 1911; de Mello-Leitão 1937; Darlington 1957; Morain 1984; Fleming 1987). During the 19th and 20th centuries, it was widely adopted and constituted the 'standard' system, especially for vertebrate taxa, although there were some modifications. For example, Heilprin (1887) considered it more appropriate to unite the Nearctic and Palearctic regions into a single region. Schmidt

(1954) rearranged the Nearctic, Palearctic, Ethiopian and Oriental regions into an Arctogean kingdom; described a Neogean kingdom (South America) and a Notogean kingdom (Australasia); and identified two transition zones, namely, Caribbean (between Arctogea and Neogea) and Celebesian (between Arctogea and Notogea). Cox (2001) accepted Wallace's zoogeographic regions, which he considered in fact to represent 'mammal zoogeographic regions', and so as to simplify their names, he suggested the following: North American region (=Nearctic), Eurasian region (=Palearctic), South American region (=Neotropical), African region (=Ethiopian), Oriental region and Australian region.

Engler (1879, 1882, 1899) provided a phytogeographical regionalisation of the world, recognising four kingdoms (Holarctic, South American, Paleotropical and Old Oceanic) and 32 regions. The Old Oceanic kingdom contrasts with the Sclater–Wallace zoogeographical system in recognising widely disjunct areas – Chile, New Zealand's South Island, the Subantarctic islands, most of Australia and South Africa – as part of a single biogeographical unit. Engler (1899) renamed this kingdom the Austral kingdom. Engler's system was widely adopted by phytogeographers, but some authors excluded South Africa and Australia from the Antarctic or Holantarctic kingdom, leaving in there only southern South America and New Zealand (Good 1947; Takhtajan 1961, 1986; Mattick 1964; Cabrera and Willink 1973), whereas others further divided this kingdom separating South America and New Zealand into different kingdoms (Drude 1884; Diels 1908). Newbigin (1950) recognised five regions for the world, as follows: Northern lands (Holarctic), Mediterranean, Northern Paleotropical Desert, Intertropical (tropics of America, Africa and eastern Asia) and Austral (southern parts of southern continents). Takhtajan (1986) provided a biogeographical phytoregionalisation of the world, recognising the following five kingdoms: Holarctic, Paleotropical, Neotropical, Cape, Australian and Antarctic (including Patagonia and New Zealand). This regionalisation has become widely used by phytogeographers. Cox (2001) considered that the recognition of the Cape kingdom is inconsistent with Takhtajan's own criteria, based on the percentage of endemic taxa (although Takhtajan did not provide figures for the total number of families or genera in the different kingdoms), by which it should be regarded as a mere province instead of a kingdom; and that the high plant diversity of the Holarctic kingdom, used to justify its treatment as a kingdom, has been inflated artificially. Additionally, he noted that different authors have included some of the remains of a once continuous southern Gondwana cool-temperate flora in an inconsistent way; and that there was a close relationship between Africa (assigned to the Paleotropical kingdom) and South America (Neotropical kingdom), so South America, Africa and India–South-east Asia should be recognised as separate kingdoms. On the basis of these critiques, Cox (2001) recognised the following five phytogeographic kingdoms: Holarctic (unchanged), African (containing also the Cape region), Indo-Pacific (including the Indo-Malesian and Polynesian subkingdoms), South American (South and Central America) and Australian (Australia and New Zealand).

Some zoogeographers proposed regionalisation schemes that differed from the Sclater–Wallace's system. Kuschel (1964)

discussed the geographical distribution of plant and animal taxa from the southern continents, and on the basis of the phylogenetic relationships of several taxa and the possibility of Antarctica being a former land-bridge, proposed an 'Austral region', to which he assigned the Patagonian, South African and Australian subregions. Rapoport (1968) recognised the following three regions for the world: the Holarctic region for the areas of the northern hemisphere, including the Nearctic and Palearctic regions of previous authors; the Holotropical region for the tropical areas of the Americas, Africa, South-east Asia and the Pacific islands; and the Holantarctic region for southern South America, South Africa, Australia, New Guinea, New Zealand and Antarctica. Smith (1983), on the basis of a numerical analysis of the mammal families of the world, recognised the following four regions and 10 subregions: Holarctic region (Nearctic and Palearctic subregions), Latin American region (Neotropical and Argentine subregions), Afro-Tethyan region (Mediterranean, Ethiopian and Oriental subregions) and Island region (Australian, West Indian and Madagascan subregions).

In addition to phytogeographical and zoogeographical regionalisations, some authors have attempted to provide general biogeographical schemes. Udvardy (1975) recognised eight biogeographic kingdoms, including Nearctic, Palearctic, Neotropical, Afrotropical, Indomalayan, Oceania, Australian and Antarctic. He grouped southern Chile, New Zealand and Tasmania into the Antarctic kingdom, but kept Australia and South Africa independent of it. Pielou (1979, 1992) provided a consensus regionalisation, combining several zoogeographical and phytogeographical systems, recognising the following eight regions: Nearctic, Paleotropical, Neotropical, Ethiopian, Oriental, Australasian, Oceanian and Antarctic. Müller (1986) recognised five biogeographic kingdoms, namely, Holarctic, Neotropical, Paleotropical, Australian and Archinotic. He also identified five transition zones, including Indonesia (Oriental–Australian transition), Central America (Neotropical–Paleotropical–Holarctic transition), southern South America (Neotropical–Archinotic transition) and southern New Zealand (Australian–Archinotic transition). Morrone (2002) proposed a general biogeographical scheme, taking into account the results of some previous track and cladistic biogeographical analyses (e.g. Schuh and Stonedahl 1986; Craw and Page 1988; Crisci *et al.* 1991; Amorim and Tozoni 1994) that have questioned the naturalness of some of the regions previously recognised, suggesting the recognition of the following three kingdoms and 12 regions: Holarctic kingdom (Nearctic and Palearctic regions), Holotropical kingdom (Neotropical, Afrotropical, Oriental and Australotropical regions) and Austral kingdom (Andean, Antarctic, Cape, Neoguinean, Australotemperate and Neozelandic regions).

More recent efforts have involved quantitative analyses of large datasets. Procheş (2005) applied a cluster analysis to species of Chiroptera, identifying 10 areas that showed some similarities with previously recognised regions, e.g. North America (=Nearctic region), Patagonia (=Andean region), temperate Eurasia (Palearctic region) and Sub-Saharan Africa (=Ethiopian region). Kreft and Jetz (2010) applied a multivariate statistical protocol to distributional data of mammal families, genera and species, and delimited 30 regions, nested into the

following six major kingdoms: Australian (Australia, New Guinea, New Zealand and New Caledonia), Neotropical (South America, Central America and the Antilles), African (subsaharan Africa, the Arabian peninsula and parts of Near and Middle East), Oriental (also including Wallacea), Palearctic and Nearctic. Procheş and Ramdhani (2012) analysed different terrestrial vertebrate taxa by using cluster analysis, finding 14 clusters of ecoregions that were constant across different analyses; these authors recognised the following regions: Arctic (northern Canada, Greenland and Arctic Eurasia), Nearctic, Palearctic, Caribbean (Antilles), Neotropical, Afrotropical, Madagascan, Indo-Malaysian, Wallacean, New Guinean, Australian, Polynesian, Andean and Antarctic. Additionally, they identified the following four transition zones, which they treated as subregions: Central American (Neotropical–Nearctic transition), La Plata (Neotropical–Andean transition), Sahero-Arabian (Palearctic–Afrotropical transition) and Sino-Himalayan (Palearctic–Indo-Malaysian transition). Holt *et al.* (2013a) combined data on the global distributions and phylogenetic relationships of 21 037 species of amphibians, birds and non-marine mammals, using pairwise phylogenetic β -diversity metrics to quantify change in phylogenetic composition among species assemblages. They identified 20 regions grouped into the following 11 larger kingdoms: Nearctic, Palearctic, Panamanian, Neotropical, Sahero-Arabian, Afrotropical, Madagascan, Sino-Japanese, Oriental, Oceanian and Australian. Kreft and Jetz (2013) considered that some of these kingdoms should be better considered as transition zones, and Holt *et al.* (2013b) responded that the distinction between kingdoms and transition zones was worthy of investigation but not justified by their analysis. Rueda *et al.* (2013) analysed presence–absence distributional data of amphibians, birds and mammals of the world using a clustering algorithm, and found that the regions delimited by using genera were nearly identical to those of Wallace, whereas two new regions based on mammals and another two based on birds coincided with Wallace's subregions. Ribeiro *et al.* (2014) analysed distributional data of species of Tipulidae (Diptera) of the world, using the endemism analysis implemented in NDM/VNDM (Goloboff 2011) and identified the following nine areas of endemism that coincided with previously identified regions or subregions: West Palearctic, Nearctic, East Palearctic–Oriental, West North America, Australia, Neotropical, Sub-Saharan Africa, Palearctic and Middle East.

There are many similarities among the reviewed phytogeographical, zoogeographical and biogeographical regionalisations. Some of the areas recognised as kingdoms or regions are fairly constant, such as, for example, the Nearctic, Palearctic, Oriental and Australian regions. In other cases, disagreements may be resolved by recognising simultaneously kingdoms and regions nested within them. For example, the Holarctic kingdom to group the Nearctic and Palearctic regions, or the Holotropical kingdom to group the Neotropical, Ethiopian and Oriental regions. In other cases, areas of basic disagreement seem more difficult to solve, especially when dealing with the possible composite nature of the southern continents. Additionally, instead of sharp boundaries, more flexible transition zones seem a better solution, as discussed by

several authors (Darlington 1957; Pielou 1979, 1992; Müller 1986; Morrone 2002; Kreft and Jetz 2013).

Revised biogeographical regionalisation of the world

The revised biogeographical regionalisation I present herein (Fig. 1) represents an attempt of consensus among previous proposals. It divides the world into three kingdoms, following Newbigin (1950), Kuschel (1964), Rapoport (1968), Morrone (2002) and Moreira-Muñoz (2007). I (Morrone 1996) previously speculated on the cladistic relationships of these kingdoms, suggesting the sequence (Holarctic, (Holotropical, Austral)). Two cladistic biogeographical analyses, one based on terrestrial and freshwater taxa (Humphries and Parenti 1999) and the other based on marine taxa (Glasby 2005), identified the same three kingdoms, although their relationships differed, being (Holotropical, (Holarctic, Austral)) for Humphries and Parenti (1999) and (Austral, (Holarctic, Holotropical)) for Glasby (2005). A future analysis considering a large and diverse array of plant and animal taxa may contribute to solving this incongruence.

Within the kingdoms, nine regions are recognised herein. They follow most of the regionalisations analysed (e.g. Sclater 1858; Wallace 1876; Good 1947; Kuschel 1964; Rapoport 1968; Pielou 1979, 1992; Müller 1986; Morrone 2002; Kreft and Jetz 2010; Procheş and Ramdhani 2012). In the boundaries between the latter, five transition zones are delimited, as formerly recognised by several authors (e.g. Müller 1986; Halffter 1987; Morrone 2006, 2014, 2015a, 2015b; Kreft and Jetz 2013).

Holarctic kingdom Heilprin (1887)

This corresponds to North America, Greenland, Europe, northern Africa and Asia north of the Himalayan mountains. It has been recognised as a region (Heilprin 1887; de Mello-Leitão 1937; Newbigin 1950; Rapoport 1968; Smith 1983) or a kingdom (Good 1947; Müller 1986; Takhtajan 1986; Cox 2001; Morrone 2002). From a palaeogeographic viewpoint, the Holarctic kingdom corresponds to the palaeocontinent of Laurasia (Morrone 2002).

Sanmartín *et al.* (2001) analysed patterns of dispersal, vicariance and diversification on the basis of the phylogenetic trees of 57 animal taxa, documenting biogeographical events from the Late Mesozoic to the present. They found phylogenetically determined biogeographical patterns, where dispersal within the Nearctic and within the Palearctic was more common than between these regions, although there were some trans-Atlantic dispersal (eastern Nearctic–western Palearctic) in the Early–Mid Tertiary.

Two regions belong to this kingdom: Nearctic and Palearctic.

Nearctic region Sclater (1858)

This region corresponds to Canada, USA, northern Mexico and Greenland (Morrone 2002). It has been treated as a region (Sclater 1858; Murray 1866; Kirby 1872; Wallace 1876; Sclater 1894; Bartholomew *et al.* 1911; Darlington 1957; Pielou 1979, 1992; Müller 1986; Morrone 2002; Escalante *et al.* 2010, 2013; Procheş and Ramdhani 2012), a subregion (Smith 1983) or a

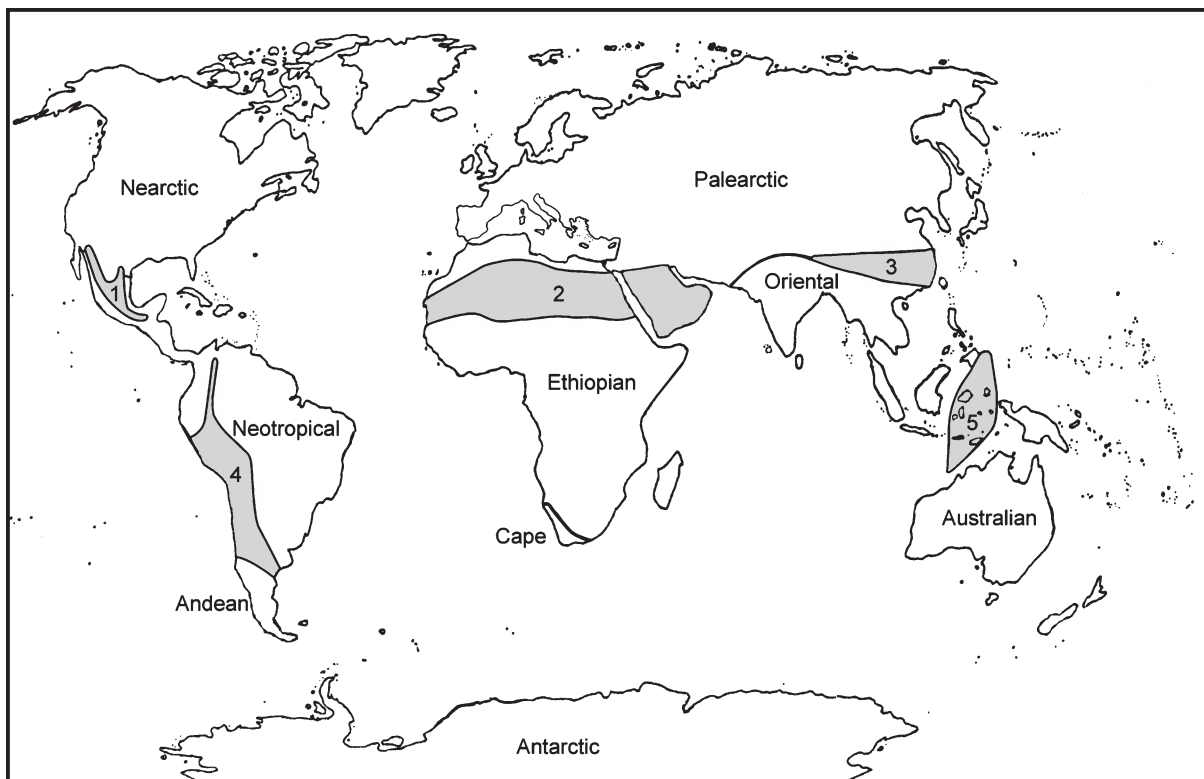


Fig. 1. World biogeographical regionalisation, with indication of the regions (white) and transition zones (grey). Transition zones: 1, Mexican; 2, Saharo-Arabian; 3, Chinese; 4, Indo-Malayan; 5, South American.

kingdom (Udvardy 1975; Morain 1984; Udvardy 1987; Kreft and Jetz 2010). Its southernmost limit is rather variable according to different authors (Udvardy 1975; Ribeiro *et al.* 2014).

Escalante *et al.* (2013) recently analysed the regionalisation of the Nearctic region on the basis of an endemism analysis of distributional models of mammal species. They recognised three subregions, namely, Canadian, Alleghanian and Californian–Rocky Mountains.

Paelearctic region Sclater (1858)

This region corresponds to Arctic and temperate Eurasia, the Mediterranean and Africa north of the Sahara, including also the islands from the Arctic, the sea of Japan, the eastern half of the North Atlantic and Macaronesia (Udvardy 1987). It has been usually treated as a region (Sclater 1858; Murray 1866; Kirby 1872; Wallace 1876; Sclater 1894; Bartholomew *et al.* 1911; Darlington 1957; Pielou 1979, 1992; Müller 1986; Morrone 2002; Procheş and Ramdhani 2012) and rarely as a subregion (Smith 1983) or a kingdom (Udvardy 1975; Morain 1984; Udvardy 1987).

Holotropical kingdom Rapoport (1968)

This corresponds to the tropical areas of the world, approximately between 30°S and 30°N. It was originally described by Rapoport (1968) as a region combining the Neotropical and Palearctic regions of previous authors and posteriorly treated as a kingdom (Morrone 2002). From a palaeogeographical viewpoint, it corresponds to the eastern portion of the Gondwana palaeocontinent (Crisci *et al.* 1993) or tropical Gondwana (Amorim *et al.* 2009).

It comprises the following three regions: Neotropical, Ethiopian and Oriental.

Neotropical region Sclater (1858)

This region corresponds to tropical South America, Central America, southern central Mexico and the West Indies. It has been treated as a region (Sclater 1858; Murray 1866; Huxley 1868; Kirby 1872; Wallace 1876; Sclater 1894; Lydekker 1896; Sclater and Sclater 1899; Bartholomew *et al.* 1911; de Mello-Leitão 1937; Darlington 1957; Kuschel 1964; Rapoport 1968; Pielou 1979, 1992; Müller 1986; Smith 1983; Cox 2001; Morrone 2002; Procheş and Ramdhani 2012), a kingdom (Engler 1882; Heilprin 1887; Diels 1908; Good 1947; Udvardy 1975; Morain 1984; Müller 1986; Takhtajan 1986; Udvardy 1987; Cox 2001; Kreft and Jetz 2010) or a subregion (Schmidt 1954).

Morrone (2014) provided a regionalisation of the Neotropical region. Three subregions are recognised, namely, Antillean, Brazilian and Chacoan.

Ethiopian region Sclater (1858)

This region corresponds to the African continent south of the Sahara (excluding South Africa), the northern part of the Arabian peninsula, Madagascar and the West Indian Ocean islands. It has been treated as a region (Sclater 1858; Murray 1866; Kirby 1872; Wallace 1876; Sclater 1894; Bartholomew *et al.* 1911; de Mello-Leitão 1937; Darlington 1957; Pielou 1979, 1992; Müller 1986; Morrone 2002; Procheş and Ramdhani 2012), a subregion (Smith

1983) or a kingdom (Udvardy 1975; Morain 1984; Udvardy 1987; Cox 2001; Kreft and Jetz 2010).

The affinities between the Ethiopian and Oriental regions led some authors to treat them as a single Palearctic kingdom (Good 1947; Müller 1986; Takhtajan 1986); however, as noted by Cox (2001), biotic affinities of the African flora lie with both the Neotropical and Oriental floras. Cox (2001) and Kreft and Jetz (2010) placed the northern boundary of the Ethiopian region much further north, but Ribeiro *et al.* (2014) situated it in the same position as did the Wallace–Sclater's system.

Oriental region Wallace (1876)

This region corresponds to the tropical areas of Eurasia and South-east Asia, comprising India, Himalaya, Myanmar, Malaysia, Indonesia, the Philippines, Micronesia, Polynesia and Hawaii (Udvardy 1975). It has been treated as a region (Sclater 1858; Murray 1866; Kirby 1872; Wallace 1876; Sclater 1894; Bartholomew *et al.* 1911; de Mello-Leitão 1937; Darlington 1957; Thorne 1964; Usinger 1964; Pielou 1979, 1992; Müller 1986; Cox 2001; Morrone 2002; Procheş and Ramdhani 2012) or a kingdom (Udvardy 1975; Morain 1984; Udvardy 1987; Cox 2001). Ribeiro *et al.* (2014) did not recover the Oriental region as a separate area, but instead merged with the East Palearctic.

The tropical Pacific islands have been assigned to the Oriental or the Australian region (Wallace 1876; Thorne 1964; Usinger 1964; Stoddart 1992), and they have been treated as a separate region by Udvardy (1975) and Holt *et al.* (2013a). They are assigned herein to the Oriental region, emphasising the tropical affinities of their biota, where they may be treated as the Polynesian subregion.

Austral kingdom Engler (1899)

This corresponds to the southern temperate areas in South America, South Africa, Australasia and Antarctica (Newbigin 1950; Kuschel 1964; Rapoport 1968; Udvardy 1975). It has been recognised as a kingdom (Engler 1882, 1899; Udvardy 1975; Müller 1986; Takhtajan 1986; Morrone 2002; Moreira-Muñoz 2007) or a region (Newbigin 1950; Kuschel 1964; Rapoport 1968). The relationships among these widely separated areas have been noted earlier by Treviranus (1803), who recognised an 'Antarctic flora' distributed in Chile, Magallanes, Tierra del Fuego and New Zealand. From a palaeogeographical viewpoint, the Austral kingdom corresponds to the western portion of the palaeocontinent of Gondwana (Crisci *et al.* 1993) or temperate Gondwana (Amorim *et al.* 2009).

Sanmartín and Ronquist (2004) examined a large dataset of plant and animal taxa by applying tree-reconciliation analysis, assessing the relative roles of vicariance and dispersal in the biogeographical evolution of the Austral kingdom. They postulated that the break-up of Gondwana has played an important role in moulding the vicariance patterns of the animal Gondwanan groups, which may be old taxa, presumably Mesozoic. Plants, in contrast, conflict with continental fragmentation patterns, so it is possible that the plant taxa analysed were too young to have been affected or they once fragmented in response to Gondwanan splits but their original patterns were subsequently lost because of dispersal and extinction events.

The Austral kingdom Engler (1899) comprises four regions, namely, Cape, Andean, Australian and Antarctic.

Cape region Grisebach (1872)

This region corresponds to the south-western portion of South Africa. It has been recognised as a separate kingdom (Good 1947; Takhtajan 1986), a subregion of the Austral region (Kuschel 1964) or a region of the Austral kingdom (Morrone 2002). Its boundaries are unclear, and some recent studies (e.g. Van Rooy and Van Wyk 2012) have suggested the existence of a Greater Cape region, including also other adjacent areas.

Rapoport (1968) postulated that the early detachment of this area from the other southern continents and the strong influence of tropical Africa have diluted its Austral relationships. The evidence provided by some recent phytogeographical analyses is contradictory. Galley and Linder (2006) found a complex pattern, with both Austral and tropical plant clades coexisting, but no conclusive evidence to separate the Cape region from the rest of the Ethiopian region. Born *et al.* (2007) evaluated Cape's plant endemism and suggested its recognition as a separate phytogeographic region. Galley *et al.* (2007) found that the Cape hosts several lineages that have evolved *in situ* and posteriorly dispersed into tropical Africa. Moreira-Muñoz (2007) analysed the affinities of the Cape region with other Austral areas, concluding that it could be excluded from the Austral kingdom. The analysis of Verboom *et al.* (2009) of dated phylogenies by using a relaxed Bayesian approach detected considerable recent speciation within the area, concluding that it hosts a mix of ancient and recently radiated groups. A zoogeographical analysis of amphibian taxa (Poynton 2000) suggested that it would be inappropriate to classify the Cape fauna as Afrotropical. Additionally, molecular phylogenetic analyses of animal taxa with poor dispersal capabilities (Giribet and Edgecombe 2006; Boyer *et al.* 2007) placed Cape taxa in an Austral clade.

Andean region Engler (1882)

This region corresponds to southern South America, extending through the Andean highlands north of this latitude. It was considered as a subregion (Wallace 1876; Sclater and Sclater 1899; Kuschel 1964; Smith 1983; Morrone 1996) or a region (Engler 1882; Good 1947; Morain 1984; Takhtajan 1986; Morrone 2002, 2006; Kref and Jetz 2010; Procheş and Ramdhani 2012). Müller (1986) identified the southernmost portion of the Andean region (the Subantarctic subregion) as a transition zone, but this is clearly not the case because of its endemic and distinctive biota (Morrone 2006).

Morrone (2015a) provided a regionalisation of the Andean region. Three subregions were recognised, namely, Central Chilean, Subantarctic and Patagonian.

Australian region Sclater (1858)

This region corresponds to Australia, New Guinea, New Caledonia and New Zealand. It was treated as a region (Sclater 1858; Murray 1866; Kirby 1872; Wallace 1876; Sclater 1894; Bartholomew *et al.* 1911; de Mello-Leitão 1937; Darlington 1957; Pielou 1979, 1992; Müller 1986; Cox 2001; Procheş and Ramdhani 2012), a kingdom (Good 1947; Morain 1984;

Müller 1986; Takhtajan 1986; Udvardy 1975, 1987; Cox 2001; Kref and Jetz 2010) or a subregion (Kuschel 1964; Smith 1983). Morrone (2002) distinguished the Australo-temperate, Australotropical, Neoguinean and Neozelandic regions, but none of the reviewed regionalisations recognised them as separate regions. Fleming (1987) has already noted the inconvenience of splitting Australia from New Zealand. They may eventually be treated as subregions.

Ebach *et al.* (2013, 2015) and González-Orozco *et al.* (2014) provided regionalisations of Australia, which would be a subregion of the Australian region, as herein delimited.

Antarctic region Grisebach (1872)

This region corresponds to Antarctica. It has been treated as a region (de Mello-Leitão 1937; Pielou 1979, 1992; Morrone 2002; Procheş and Ramdhani 2012) or a kingdom (Udvardy 1975, 1987; Takhtajan 1986).

Most of the Subantarctic islands do not belong to this region. The Snares, Auckland, Campbell and Chatham Islands belong to the Australian region (New Zealand subregion), and the Falkland Islands to the Andean region (Subantarctic subregion) (Morrone 1998). Kerguelen, Heard, Crozet, Marion and Prince Edward Islands (Indian Ocean) belong to the Ethiopian region. Tristan da Cunha, Gough, Inaccessible and Nightingale Islands (Atlantic ocean) have no clear relationships.

Transition zones

In the boundaries between the regions, five main biogeographic transition zones are recognised (Fig. 1):

The Mexican transition zone includes the mountainous areas of Mexico, Guatemala, Honduras, El Salvador and Nicaragua (Darlington 1957; Halffter 1964, 1974, 1976, 1978, 1987; Palestini and Zunino 1986; Morrone 2006, 2014, 2015b; Riddle and Hafner 2010). It corresponds to the boundary between the Nearctic and Neotropical regions, and comprises the Sierra Madre Occidental, Sierra Madre Oriental, Sierra Madre del Sur, Transmexican Volcanic Belt and Chiapas Highlands provinces (Morrone 2006, 2014, 2015b).

The Saharo-Arabian transition zone comprises the Sahara desert and the Arabian peninsula (Müller 1986; Kref and Jetz 2013). It corresponds to the boundary between the Palearctic and Ethiopian regions. Müller (1986) provided some examples of taxa from this transition zone.

The Chinese transition zone (Palestrini *et al.* 1985; Müller 1986; Kref and Jetz 2013) corresponds to the boundary between the Palearctic and Oriental regions. Palestini *et al.* (1985) analysed the geographical distribution of some groups of Scarabaeoidea (Coleoptera) of this area, detecting Palearctic, Oriental and Sino-Japanese biotic affinities.

The Indo-Malayan, Indonesian or Wallace's transition zone (Darlington, 1957; Müller 1986; Kref and Jetz 2013) corresponds to the boundary between the Oriental and Australian regions. Müller (1986) discussed its boundaries and gave examples of Oriental and Australian taxa with overlapping distributions in this transition zone.

The South American transition zone comprises the Andean highlands between western Venezuela and northern Chile and central western Argentina (Morrone 2004, 2006, 2014, 2015a).

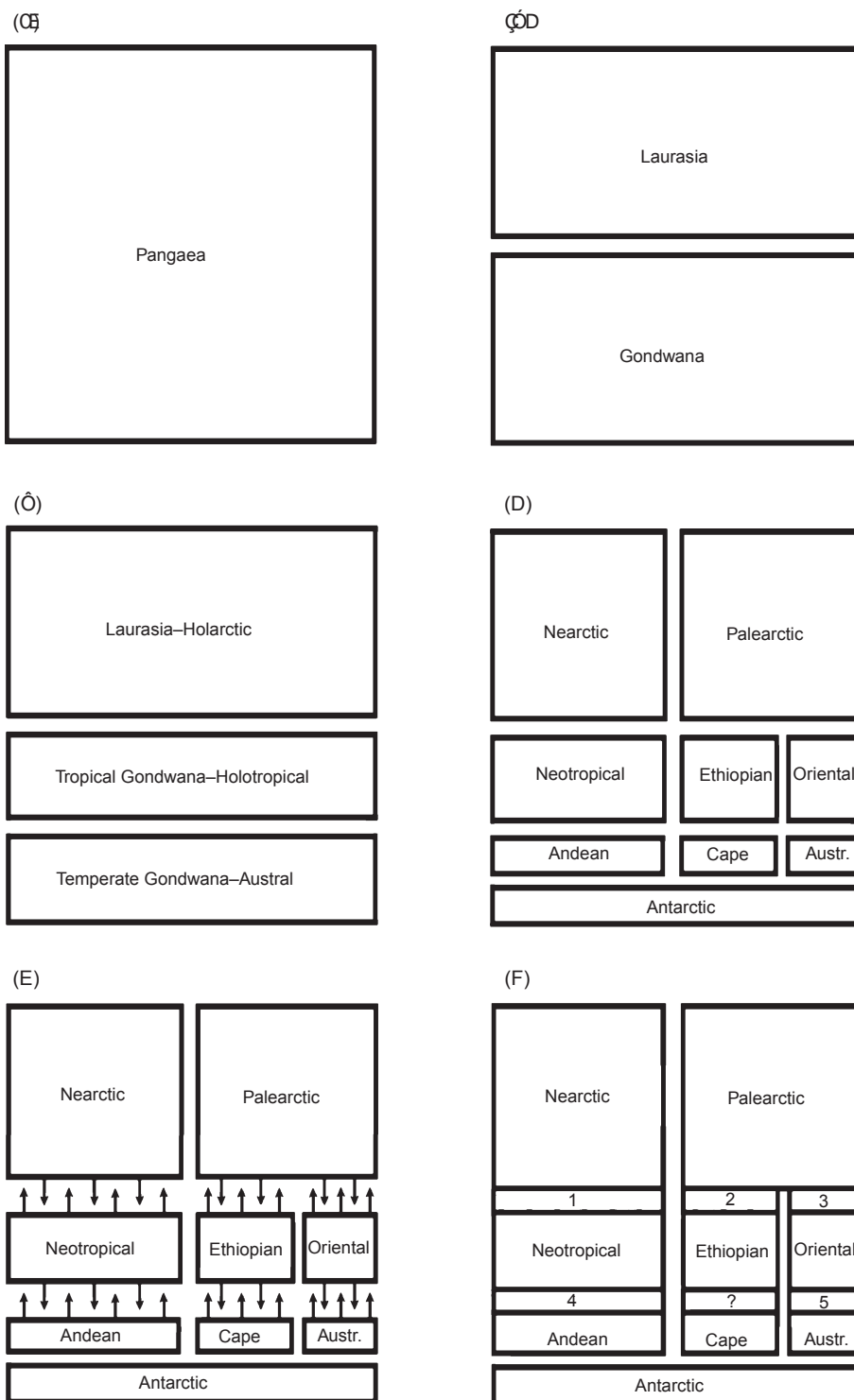


Fig. 2. Schematic diagram of the dispersal-vicariance model implied by the biogeographical regionalisation herein proposed, with indication of the regions (white) and transition zones (grey). A–C. Vicariance events leading to the distinct biotas of the three kingdoms (Jurassic). D. Vicariance events leading to the distinct biotas of the nine regions (Early Cretaceous–Paleogene). E, F. Geodispersal events leading to the mixed biotas of the transition zones (Tertiary). Transition zones: 1, Mexican; 2, Saharo-Arabian; 3, Chinese; 4, Indo-Malayan; 5, South American.

It corresponds to the boundary between the Neotropical and Andean regions, which was analysed by Rapoport (1968), who discussed the alternative placements given by different authors to the 'subtropical line' that separates both regions (see also Ruggiero and Ezcurra 2003). Urtubey *et al.* (2010) analysed the distribution of some Asteraceae of this transition zone.

A South African transition zone, which would correspond to the boundary between the Ethiopian and Cape regions, has not been proposed yet. The mix of varied groups in South Africa (e.g. Verboom *et al.* 2009) may point to the existence of such area; however, its proper demarcation is out of the scope of the present analysis.

Patterns, processes and predictions

The proposed biogeographical regionalisation can be expressed as a dispersal–vicariance model (Fig. 2), with two main processes involved, namely, vicariance and geodispersal. On the basis of this model, the following three primary hypotheses may be formulated:

- HI. The biotas characteristic of the three kingdoms were isolated by vicariant events that occurred mostly during the Jurassic (Fig. 2A–C).
- HII. The biotas characteristic of the nine regions were isolated by vicariant events that occurred from the Early Cretaceous to the Paleogene (Fig. 2D).
- HIII. The biotas characteristic of the transition zones were assembled by dispersal events that occurred during the Tertiary (Fig. 2E, F).

From the primary hypotheses, a set of secondary hypotheses may be deduced for specific areas, as follows:

- H1. Taxa from the Nearctic and Palearctic regions are phylogenetically more closely related to each other than they are to those of other regions.
- H2. Taxa from the Neotropical, Ethiopian and Oriental regions are phylogenetically more closely related to each other than they are to those of other regions.
- H3. Taxa from the Andean, Cape, Australian and Antarctic (fossils) regions are phylogenetically more closely related to each other than they are to those of other regions.
- H4. Taxa from the Mexican transition zone are phylogenetically related to either Nearctic or Neotropical taxa, rather than to taxa of other regions.
- H5. Taxa from the Saharo-Arabian transition zone are phylogenetically related to either Palearctic or Ethiopian taxa, rather than to taxa of other regions.
- H6. Taxa from the Chinese transition zone are phylogenetically related to either Palearctic or Oriental taxa, rather than to taxa of other regions.
- H7. Taxa from the South American transition zone are phylogenetically related to either Neotropical or Andean taxa, rather than to taxa of other regions.
- H8. Taxa from the Indo-Malayan transition zone are phylogenetically related to either Oriental or Australian taxa, rather than to taxa of other regions.

From the primary and secondary hypotheses, specific biogeographical and phylogenetic predictions can be made and

tested. These predictions can refer to the biogeographical distribution of the taxa inhabiting specific kingdoms, regions and transition zones; the phylogenetic placement of their related taxa; and the minimum dates of origin of their characteristic clades. Phylogenetic hypotheses, fossil information and molecular clocks may allow tests of these predictions.

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