



The Austral floristic realm revisited

A. Moreira-Muñoz*

Institute of Geography, University of Erlangen-Nürnberg, Kochstrasse 4/4, 91054 Erlangen, Germany

Abstract

The classification of the Earth's flora into floristic regions has been the major goal of plant geography since the 19th century. A detailed revision of 19th and 20th century classifications is presented herein, with particular emphasis on the delimitation of the Austral floristic realm. A comparison between Chile, New Zealand, and the Cape Floristic Region is made at the genus level. Using the vascular flora of these biogeographical regions, the analysis revises previous attempts to define the Austral realm, while also assessing differences made by changes in taxonomic delimitations from recent molecular phylogenetic studies. The results indicate that the Austral floristic realm can nowadays be better described as a circum-Antarctic generalized track, composed of some 60 genera and 15 families restricted to South America and Australasia, possibly including South Africa.

Keywords

Antarctica, Australasia, biogeographical classification, Cape Floristic Region, Chile, floristic kingdom, New Zealand, panbiogeography, South Pacific track, southern South America.

*Correspondence: Andrés Moreira-Muñoz, Instituto de Geografía, P.Universidad Católica de Chile, Av. Vicuña Mackenna 4860, Santiago, Chile.
E-mail: amoreira@geo.puc.cl

INTRODUCTION

In historical biogeography significant developments are often reached through continuously challenging the parameters of biogeographical classifications. Cox (2001) discussed the many inconsistencies in previous schemes and provided a new global system of six phytogeographical kingdoms and another of six mammal zoogeographical regions. While commenting on this last scheme, Morrone (2002) proposed an integrated biogeographical scheme for all organisms composed of three kingdoms: a Holarctic kingdom, a Holotropical kingdom, and an Austral one. Morrone (2002) and Cox (2001) recognized a lack of studies that compare the composition of different floras, especially 'in the case of that most surprising unit, the Antarctic kingdom, spread over several areas that are widely separated geographically' (Cox, 2001, pp. 511–512). It seems appropriate, therefore, to reanalyse the floristic relationships of the southern territories.

THE BIOGEOGRAPHICAL CLASSIFICATION OF THE AUSTRAL TERRITORIES

Augustin Pyramus de Candolle (1778–1841) was the first naturalist to notice that regions exist that are distinct from one

another because they contain plants that are restricted to that area, for which he coined the word 'endemic' (Cox & Moore, 2005, p. 22). Following this observation, a major goal of floristic plant geography has been the classification of the Earth into floristic areas. A. P. de Candolle wrote '[...] from all these facts, one may deduce that there are botanical regions; and by this term I denote whatever areas that, with the exception of introduced species, have a certain number of plants that to them are peculiar, and that can be called aboriginal' (quoted by Nelson, 1978, p. 283). Since then, there has been controversy over the most adequate global classification, and in particular, contrasting views have been put forward for the Southern Hemisphere. A summary of floristic classifications since the beginnings of plant geography is given in Table 1 and is discussed hereafter.

Gottfried R. Treviranus (1776–1837), one of the first naturalists to use the term 'biology', put forward a pioneering global floristic classification, dividing the world's flora into eight main floras (*Hauptfloren*). This early classification included an Antarctic flora (*Antarktische Flor*), which comprised Chile, Magallanes, Tierra del Fuego, and New Zealand (Treviranus, 1803). The Cape flora was included in an *Afrikanische Flor*. Treviranus was, to my knowledge, the first biologist to recognize explicitly the floristic relationship between southernmost South America and New Zealand,

Table 1 Summary of floristic classifications for southern South America, New Zealand and the Cape Region since the beginnings of plant geography.

Source	No. of realms	No. of regions	Southern South America	New Zealand	Cape Floristic Region
Treviranus, 1803	8	–	Antarktische Flor	Antarktische Flor	Afrikanische Flor
Augustin Pyramus de Candolle, 1820	–	20	Le Chili and les terres Magellaniques	(Not explicitly mentioned)	Le cap de Bonne-Espérance, ou l'extrémité australe de l'Afrique, hors des tropiques
Schouw, 1823	25	–	South of 42°: Antarktisches Florenreich; 42°–23°: Reich der Holzartigen Synanthereen [Compositae]; north of 23°: Reich der <i>Cactus</i> und <i>Piper</i>	Neuseeländisches Florenreich	Capland: Reich der Stapelien [Apocynaceae] und Mesembrianthemem
Alphonse de Candolle, 1835	–	45	Le Chili (region 35), and la Patagonie, la terre de Feu et les iles Malouines (region 36)	Region 15 La Nouvelle-Hollande (Australia), l'île de Van Diémen (Tasmania), la Nouvelle-Zélande, la Nouvelle-Calédonie, l'île de Norfolk	Region 40, le cap de Bonne-Espérance
Grisebach, 1872	–	24	Tropical Andean flora: north to 23°; Chilenisches Übergangsgebiet: 23°–34°; Antarktisches Waldgebiet: 34°–56°	Oceanische Inseln	Kapland
Engler, 1879; Engler, 1882	4	31	Südamerikanische Florenreich: north of 41°S; Altoceanisches Florenreich : south of 41°S	Altoceanisches Florenreich: temperate New Zealand; Paläotropisches Florenreich: tropical New Zealand	Altoceanisches Florenreich: Gebiet des Caplandes
Drude, 1884	14	55	South of 41°: Antarktisches Florenreich; north of 41°: Andines Florenreich	Neuseeländisches Florenreich	Florenreich von Südafrika
Drude, 1890	14	55	Andines Florenreich and Antarktisches Florenreich	Melanesisch- Neuseeländisches Reich and Antarktisches Florenreich	Südafrikanisches Florenreich
Diels, 1908	6		Neotropis and Antarktis	Palaeotropis	Capensis
Good, 1974; (1947)	–	37	Antarctic kingdom, Patagonian region, south of 41°; Neotropical kingdom, Andean region, north of 41°	Antarctic kingdom, New Zealand region	South African kingdom, Cape Region
Mattick, 1964	6	43	South: Antarktisches Florenreich; north: Neotropisches Florenreich	South of 45°: Antarktisches Florenreich; north of 45°: Paläotropisches Florenreich	Kapländisches Florenreich
Takhtajan, 1961	6	37	Antarctic kingdom, Patagonian region, south of 40°; Neotropical kingdom, Andean region, north of 40°	Antarctic kingdom, New Zealand region	Cape kingdom
Takhtajan, 1986	6	35	Holantarctic kingdom, Chile-Patagonian region, south of 25° to Antarctic peninsula and Malvinas Islands (Falkland Is.)	Holantarctic kingdom, New Zealand region	Cape kingdom
Cox, 2001	5	–	South American kingdom	Australian kingdom	African kingdom
Morrone, 2002	3	12	Austral kingdom, Andean region	Austral kingdom, Neozelandic region	Austral kingdom, Cape or Afrotperate region

based on the early works of Molina, Forster, and Banks. Treviranus noticed also the existence of an antitropical floristic element, i.e. genera present in temperate areas from both hemispheres but absent in the Tropics, such as *Pinguicula*, *Salix*, [*Notho*]*Fagus* and *Ribes*. These relationships appeared to him surprising because at that time the known flora of Tierra del Fuego was composed of less than 40 species (Treviranus, 1803, p. 132)!

At this early stage, biogeographical representation was non-existent. Two years later, in 1805, Jean B. Lamarck and Augustin Pyramus de Candolle published the 'first biogeographical map' for the third edition of the *Flore française* (Ebach & Goujet, 2006). A.P. de Candolle further classified the world flora into 20 floristic regions (de Candolle, 1820), but this scheme still lacked a map. In 1823, Danish botanist Joakim Frederik Schouw (1789–1852) published the first phytogeographical world map (Schouw, 1823; Mennema, 1985). Schouw proposed 25 floristic kingdoms or realms (*Florenreiche*). In his scheme, South America was divided into an Antarctic and a tropical realm (*Reich der Holzartigen Synanthereen*), and New Zealand and the Cape Region were awarded the status of realm (Table 1).

One of the key naturalists contributing to the growing botanical knowledge in the middle of the 19th century was J.D. Hooker (1817–1911). While sailing on board James Cook's *Endeavour*, he notably improved the floristic knowledge of the Southern Hemisphere (Hooker, 1844–1860). Hooker's publications were almost as epoch-making as Darwin's *The Origin of Species* (Thiselton-Dyer, 1909).

Adolf Engler (1844–1930), one of the most prominent scientists in botanical history, working at the Botanical Garden in Berlin, was one of the first to try to describe a synthesis of the evolution of the plant world on the Earth's surface (Engler, 1879, 1882). He divided the world flora into four realms and 32 regions. He further divided each region into diverse provinces, and some provinces into districts (*Bezirke*), thus constructing a very detailed hierarchical system that formed the base for all following classification systems. Engler's *Altoceanisches Florenreich* grouped southern Chile with New Zealand's South Island, the sub-Antarctic islands, most of Australia and Africa's Cape Region. 'Engler was surprisingly perceptive in realizing that, scattered over the islands and lands of the southernmost part of the world, lay the remains of a single flora, which he called "the Ancient Ocean" flora. It was over 80 years before acceptance of the movement and splitting of continents at last explained this very surprising pattern of distribution' (Cox & Moore, 2005, p. 26). Later, Engler suggested that *Australe Florenreich* would be a better name as it is characterized by the *Austral-antarktischen Florenelement* (Engler, 1899, p. 149).

Oscar Drude (1852–1933) from the Botanical Garden in Dresden worked closely with Engler. Drude found several difficulties in synthesizing the floristic knowledge of his predecessors with the growing ecological knowledge as systematized by Grisebach (1872). Drude's first publication, *Die Florenreiche der Erde*, was based on a floristic approach

(Drude, 1884). He therefore defined 14 floristic kingdoms and 55 floristic regions (*Gebiete*). In this scheme, southern South America was classified in an *Antarktisches Florenreich*, New Zealand and surrounding islands in a *Neuseeländisches Florenreich*, and the Cape Region in a *Südafrikanisches Florenreich*. Drude's concern about the floristic and ecological differences soon led him to publish separate maps for floristic classification and for vegetation classification (Drude, 1887). He restated Schouw's original idea, which was to raise the African Cape Region to the category of a floristic realm.

At the beginning of the 20th century, Ludwig Diels (1874–1945), the successor of Engler in Berlin, synthesized Drude's classification into six floristic realms. He divided Engler's *Altoceanisches Florenreich* into an *Antarktis*, an *Australis* and a *Capensis* (Diels, 1908). He considered the *Australis* as comprising Australia and Tasmania, and considered Melanesia and New Zealand as part of the *Paläotropis*. Southernmost South America retained its designation as a realm, the *Antarktis*. Diels' small but successful book had been reprinted five times by 1958, and his realm classifications were retained (with the addition only of more detail at the regional scale) by Mattick (1964) and later popular authors such as Good (1974) and Takhtajan (1986).

English botanist Ronald Good's (1896–1992) *The Geography of the Flowering Plants* (Good, 1974) was to become one of the most popular books in the field, reaching four editions and two reprints between 1947 and 1974. In the first edition of his book he avoided the problem of the floristic kingdoms, concentrating his attention on the regions, but in the last edition he elaborated on Diels' six realms, further dividing them into 37 regions. Good proposed that the Cape Region merited the status of a realm and that the Antarctic kingdom was composed of southern South America and New Zealand. The scheme is very similar to that of the Russian botanist Armen Takhtajan (1910–), which also became very popular after its translation into English. Takhtajan first maintained the six realms from Diels and the 37 regions from Good (Takhtajan, 1961), but in his most popular later work he reduced the number of regions to 35 (Takhtajan, 1986). Takhtajan's Holantarctic kingdom comprised New Zealand and the surrounding islands, Patagonia and the Juan Fernández islands. The Cape Region was also treated as a kingdom (*Capensis*).

The scheme of six floristic realms proposed by Diels (1908) and modified only at the regional scale by later authors stayed basically unchanged during the 20th century. It was only at the beginning of this century that Cox (2001) reanalysed both the floristic and faunistic long-standing schemes. With the principle that 'floral kingdoms, like zoogeographic regions, must be areas of similar size, compact and easily defined' (Cox, 2001, p. 520), he disintegrated the earlier scheme and suggested that each scattered, fragmented, and relictual area 'should, then, be allocated to whatever kingdom it is now adjacent to, its definition of description in each case containing a mention of its history' (Cox, 2001, p. 518). Chile-Patagonia should become a region of the Neotropical kingdom, New

Zealand should be transferred to the Australian Floral kingdom, and the Cape Region to the African kingdom.

In a reply to Cox (2001), Morrone (2002) challenged Cox's proposal and combined floristic and faunistic knowledge into one synthetic classification. The result is a scheme of only three biotic realms: the Holarctic kingdom, the Tropical kingdom (=East Gondwana), and the Austral kingdom (=West Gondwana). Morrone (2002) related the classification to the history of these biotas, as was Engler's early intention (1879, 1882). In fact, the result is remarkably similar to Engler's, the only difference being that Morrone groups the palaeotropics and neotropics into one Tropical realm. In Morrone's proposal the Austral kingdom is composed of southern Australia, New Zealand, South Africa and southern South America, extending through the Andes to Colombia.

Morrone did not provide an explicit account of biotic similarities between the territories classified in the Austral kingdom; the comparison below helps to fill this gap. Specifically, the floras of several Chilean regions, the Cape Region, and New Zealand will be compared. Since we are dealing with territories of different size and containing different numbers of genera, the most appropriate representation is to use a similarity index; in this case I used Jaccard's similarity index (Cox & Moore, 2005, p. 236).

FLORISTIC SIMILARITY

Explicit floristic comparisons between South America and Africa have concentrated on the tropical zone (e.g. Gentry, 1993). Other comparisons between mediterranean-climate regions lack information for South America/Chile (Beard *et al.*, 2000) or concentrate on diversity patterns rather than floristics (e.g. Cowling *et al.*, 1996). More fruitful comparisons have been made between southern South America and Australasia (Hooker, 1844–1860; Engler, 1882; von Ihering, 1891; Skottsberg, 1915, 1960; Godley, 1960; van Steenis, 1962; Moore, 1972; Wardle *et al.*, 2001).

Of crucial importance for the definition of an Austral realm are the floristic affinities, analysed on the basis of clades (*sensu* Galley & Linder, 2006), or on the basis of traditional taxonomic units, i.e. genera and families (*sensu* Good, 1974).

Floristic statistics for Chile, the Cape Region and New Zealand are shown in Table 2. The Cape Region harbours by far the richest flora at the family and genus level, and also contains a remarkable level of endemism: five endemic families

Table 3 Compared territories, number of shared genera, and Jaccard's similarity. Data sources as for Table 2.

Regions	No. of shared genera	Jaccard's similarity
CL/NZ	173	0.16
CL/CFR	150	0.09
NZ/CFR	113	0.09

and 160 endemic genera. The Chilean vascular flora contains two endemic families and 67 endemic genera. New Zealand does not harbour an endemic family, but comprises 48 endemic genera. The Cape Floristic Region (CFR) is by far the richest region at the genus level (994 genera). The floristic relationships at the generic level between Chile, the Cape Region and New Zealand are shown in Table 3.

The Chilean and New Zealand floras have 173 native genera in common; Chile (CL) shares 150 genera with CFR; and New Zealand (NZ) shares 113 genera with CFR. The three territories have 81 genera in common. Most of these latter genera have a wide distribution around the globe, i.e. are subcosmopolitan or pantropical genera (e.g. *Euphorbia*, *Gleichenia*, *Isoetes*, *Ranunculus*, *Senecio*, *Viola*) (see Appendix S1 in the Supplementary Material). 92 genera are shared between CL and NZ but not CFR; 69 are common to CL and CFR but not to New Zealand; and 32 are common to NZ and CFR but are not present in CL. Jaccard's similarity index shows almost twice the value between CL and NZ (=0.16) as between CL and CFR or CFR and NZ (=0.09) (Table 3). A list of shared genera and their presence in each territory is given in Appendix S1.

The Chilean flora is, of course, not equally distributed within the long national territory, and for a more detailed assessment three subterritories were selected. These are the Antofagasta region (ANT), located in the northern subtropical arid zone, the Coquimbo and Biobío regions under the influence of a mediterranean-type climate, and the Magallanes (MAG), the southernmost temperate region. For analytical purposes, the two small administrative regions (Coquimbo + Biobío) representing the limits of the mediterranean-type climate in Chile are grouped into one region (MED) (Fig. 1). The regions analysed are dissimilar in area and in numbers of native genera (e.g. MED = 590 genera, ANT = 315). MAG shows the lowest generic richness, namely 251 (Table 4).

Table 2 Austral vascular plant floras.

Territory	Abbreviation	Latitudinal range	Area (km ²)	Native families/genera	Endemic families/genera	Source
Chile	CL	17.6°–56°S	756,950	179/813	2/67	Moreira-Muñoz, in prep.
Cape Floristic Region	CFR	31°–34°30'S	90,000	178/994	5/160	Goldblatt & Manning, 2000
New Zealand	NZ	34°–47°S	268,680	138/439	0/48	CHR Allan Herbarium, Landcare Research, May 2006; Wilton & Breitwieser, 2000

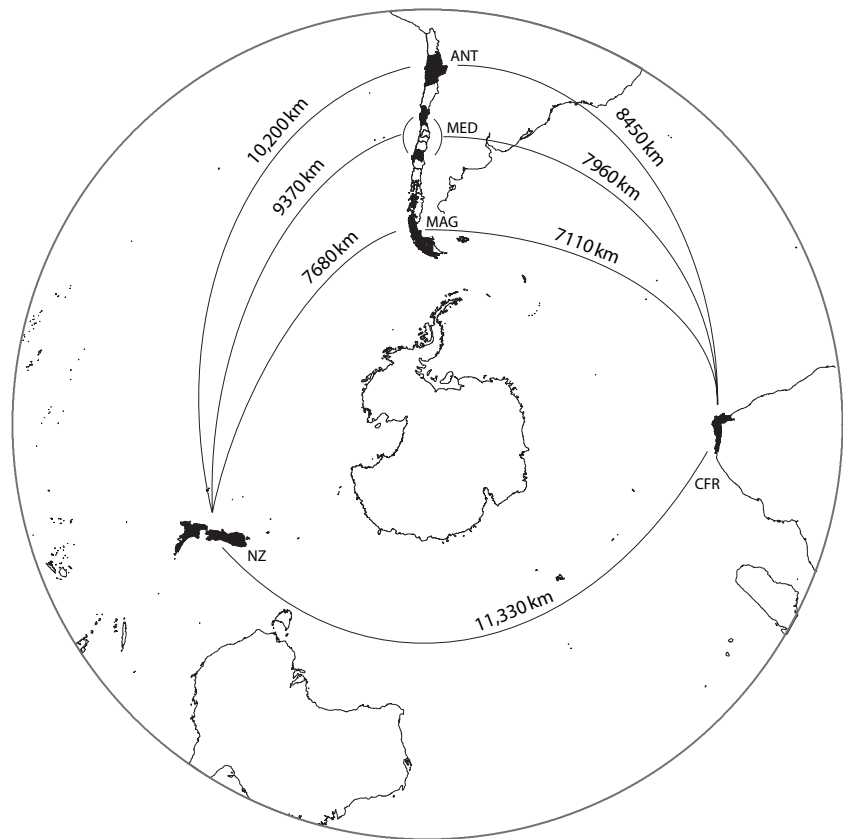


Figure 1 Southern Hemisphere south of 15°S in gnomonic projection. Geographic distance between compared territories as great-circle distance [km].

Table 4 Chilean regions included in the similarity analysis, area, and numbers of native vascular plant genera.

Chilean region	Abbreviation	Latitudinal range	Area (km ²)	No. of native genera	Source
Antofagasta	ANT	21°–26°S	126,049	315	Marticorena <i>et al.</i> , 1998
Coquimbo + Biobío	MED	29°–32°S + 36°–38.5°S	77,643	590	Marticorena <i>et al.</i> , 2001; R. Rodríguez, personal communication
Magallanes	MAG	49°–56°S	132,033	251	Henríquez <i>et al.</i> , 1995

In Table 5 the number of shared genera between regions, Jaccard's similarity and geographic distance are summarized. Similarity is usually assumed to be dependent on geographic distance, and therefore floristic similarity is plotted against the geographic distance in Fig. 2. Jaccard's distances show a trend of decreasing floristic similarity in relation to the geographic distance along the latitudinal gradient in Chile (Fig. 2). Likewise, the similarity analysis between Chilean regions and NZ shows a decrease with distance. Remarkably, the similarity index results are almost equal between ANT/MAG and MAG/NZ. NZ shares more genera with MAG (113) than MAG does with ANT (99), in spite of a doubling of the distance over the Pacific Ocean. Jaccard's similarity is lower between Chilean regions and CFR. As could be expected, the highest (but still relatively low) similarity between the Chilean regions and CFR is in MED/CFR, since both regions share a mediterranean-type climate.

AUSTRAL = ANTARCTIC

The arc-circle distance between MAG and NZ is about 7680 km. The distance along the latitudinal gradient between MAG and ANT in Chile is about 3220 km. A propagule has to cross more than twice the distance of ocean waters to reach NZ from MAG (or vice versa) as it needs to reach ANT from MAG (or vice versa) via terrestrial dispersal. In the Early Jurassic, when the southern territories were still forming the supercontinent of Gondwana, the distance between Chile and NZ might have been almost half of what it is today. Most plate tectonic reconstructions place South America and New Zealand on opposites side of Gondwana. In contrast, in the palaeoreconstructions developed under the theory of an expanding Earth (Shields, 1998; McCarthy, 2003, 2007), South America and New Zealand/Australia share a common border. Independent of the palaeogeographic scenario, the Antarctic

Table 5 Pairs of regions, the number of shared genera, Jaccard's similarity, and the geographic distance between them. The geographic distance between the Chilean regions is calculated between the centroid of each region. The geographic distances between Chilean regions and New Zealand/the Cape Region are calculated as great-circle distances [http://www.movable-type.co.uk/scripts/LatLong.html]. Data sources as for Tables 2 and 4.

Regions	No. of shared genera	Jaccard's similarity	Geographic distance
ANT/MED	250	0.38	1150
ANT/MAG	99	0.21	3220
ANT/NZ	65	0.09	10,200
ANT/CFR	71	0.06	8450
MED/MAG	194	0.30	2100
MED/NZ	134	0.15	9370
MED/CFR	124	0.08	7960
MAG/NZ	113	0.20	7680
MAG/CFR	74	0.06	7110

palaeofloras (Poole *et al.*, 2003) indicate that the ancestors of today's flora should have been much more widespread in the Late Cretaceous. Indeed, many of the elements found today in the southern continents can be traced to the Gondwana era, as a once continuous cool-temperate flora now scattered into a relict distribution by tectonic movements. Furthermore, some authors like to speak of the Austral floras as a 'Gondwanan element' (Barlow, 1981; Nelson, 1981). Antarctica was covered by forests from the Permian onwards (Taylor *et al.*, 1992). In the Early Cretaceous, the Antarctic forest ecosystem was dominated by a conifer-fern community similar to that found in the warm temperate rainforests of present-day New Zealand (Falcon-Lang *et al.*, 2001). During the Late Cretaceous, flowering plants radiated throughout Gondwana, changing the vegetation to one more similar to the angiosperm-dominated cool temperate Valdivian rainforests of present-day Chile: Nothofagaceae, Myrtaceae, Eucryphiaceae/

Cunoniaceae, Lauraceae, Monimiaceae, Araucariaceae, Cupressaceae, and Podocarpaceae (Poole *et al.*, 2003; and references therein). To this impressive record it is possible to add Late Cretaceous fossil flowers related to extant Winteraceae (Eklund, 2003).

The Antarctic forests were ultimately eradicated through global climate cooling during the Tertiary (Francis & Poole, 2002). The nature and timing of the extinctions caused by this climate cooling are still being debated, owing to the paucity of Neogene fossil sites (Ashworth & Cantrill, 2004). The extinction may have followed the mid-Miocene warm interval at *c.* 17 Ma or a mid-Pliocene warm interval at about 3 Ma (Ashworth & Cantrill, 2004). It has been suggested that, at least in the de-glaciated coastal areas of Antarctica and over the Antarctic Peninsula, a shrub tundra dominated until the Pliocene (Haywood *et al.*, 2002). In southern South America, there was a constant exchange of Neotropical and Antarctic floras throughout the Cenozoic (Troncoso & Romero, 1998; Hinojosa & Villagrán, 2005).

ORIGINS OF THE AUSTRAL FLORA

Cox (2001) queries whether the Austral region, which is scattered, fragmented, and relictual, is a natural classification. He claims that it is not convenient to include such an Austral region – because of its complexity – in a simple and consensual system. Cox (2001, p. 518) explains clearly the difficulties in the delimitation of an Austral floristic realm: 'This situation provides a biogeographic dilemma, which has so far been confronted only in superficial and inconsistent fashion by including some areas in the Antarctic floral kingdom, but not others ... Neither Good nor Takhtajan includes eastern Tasmania, the mountainous parts of eastern Australia and New Guinea, or New Caledonia, in the Antarctic Floral kingdom, despite the presence of Antarctic Floral elements in these areas'. Cox suggests that 'each of these areas should, then, be allocated to whatever kingdom it is now adjacent to, its definition or

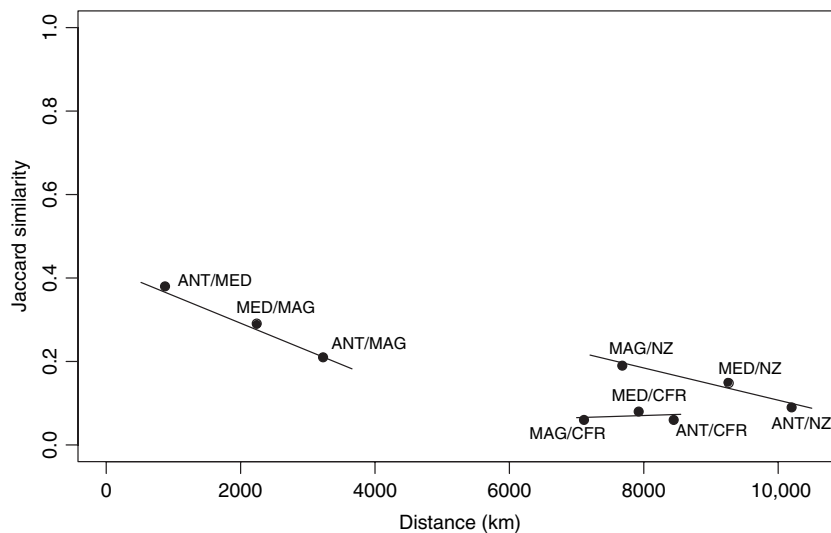


Figure 2 Geographic vs. Jaccard's distance of compared territories (ANT: Antofagasta, CFR: Cape Floristic Region, MED: mediterranean central Chile, MAG: Magallanes, NZ: New Zealand). Data source: Table 5.

description in each case containing a mention of its history. The Chile-Patagonian Region would accordingly become a region of the Neotropical kingdom... In contrast, the Flora of New Zealand is, according to Pole (1994), basically of an Australian character, the present evergreen forests having only become established since the late Tertiary or early Pleistocene, most or all of it by long-distance dispersal. Accordingly, New Zealand and its surrounding islands should be transferred to the Australian floral kingdom' (Cox, 2001, p. 518).

Recent geophysical research seems to support geographical scenarios of long-distance dispersal across the southern seas (Muñoz *et al.*, 2004). Muñoz *et al.* (2004) suggest that wind connectivity explains the biogeographical similarities in the Southern Hemisphere for groups known as 'good dispersers', such as lichens, mosses, and ferns. They suggest that this could also apply for angiosperms with very small propagules, such as orchids. In fact, many fern taxa are shared between Chile, New Zealand and the Cape Region at the generic level (*Asplenium*, *Blechnum*, *Grammitis*, *Lycopodium*) (Appendix S1), and some between Chile and New Zealand even at the species level (e.g. *Shizaea fistulosa*, *Hymenophyllum ferrugineum*). At the genus level, however, only *Rumohra* is strictly circumaustral, and all the other genera have a (sub)cosmopolitan (e.g. *Asplenium*, *Blechnum*) or pantropical (e.g. *Gleichenia*, *Grammitis*) distribution. Similarity in the relatively old fern group may actually be the result of ancient vicariant events (for a discussion see Wolf *et al.*, 2001). For orchids, there is no one single genus shared between the seven Chilean genera and the 36 native New Zealander orchid genera, challenging the supposed good dispersal ability of the family, which is based on their tiny seeds. Van Steenis (1962, p. 294) argued: 'Although dispersal of orchids may seem easy by the large amount of dust seed, successful establishment may depend on presence of its mycorrhizal fungus and insects for pollination. That the three of them, fungus spores, seeds, and insects, will travel together over long distances by chance is utterly unlikely'. Even genera that superficially appear to be good dispersers, like the ones pertaining to the Asteraceae, are not necessarily so. Of the eight Asteraceae genera shared between Chile and New Zealand, five lack a pappus suited for wind dispersal (*Abrotanella*, *Centipeda*, *Cotula*, *Lagenophora* and *Leptinella*). From a dispersalist point of view one would expect specific adaptations for wind dispersal. This is why Heads (1999) challenged the hypothesized long-distance dispersal explanation proposed by Swenson & Bremer (1997) for *Abrotanella* (see also Wagstaff *et al.*, 2006).

The claim that most of the biota shared by NZ and South America originated by means of long-distance dispersal (as proposed by Pole, 1994; Winkworth *et al.*, 2002; McGlone, 2005; Waters & Craw, 2006) seems to be overemphasized. Waters & Craw (2006) and Treweek *et al.* (2007) preferred the dispersal scenario based mainly on geological evidence, but they also recognized that at present there is insufficient geological evidence to demonstrate compellingly total Oligocene immersion of NZ, which is the basic argument for a relatively recent arrival of the biota. The processes operating in shaping current biogeographical patterns might rather be

a mix of dispersal and vicariance processes operating on different time-scales (Sluys, 1994). Michaux (2001) argued that the opposition of vicariance and dispersal is an artifact of poorly defined concepts, and suggests in place of this simplified dichotomy the recognition of five processes – modification, movement, mixing, splitting and juxtaposition – that are not logically equivalent as they operate on different time-scales. Sluys (1994) argues that none of the palaeogeographic models is fully compatible with all geological and biogeographical data available at present, and stressed that 'biogeographic data and theories should not be made subservient to geological theories but that both biological and geological information should shed their light in the causal explanation of trans-Pacific organismal tracks' (Sluys, 1994, p. 42). Interestingly, while specifically testing the directional dispersal in the Southern Hemisphere, Sanmartín *et al.* (2007) could not find the expected influence of circumpolar currents on dispersal events. The authors gave two possible explanations of their failure to detect significant patterns: (1) insufficient sample size of phylogenies that include South American taxa; or (2) that dispersal is as likely to be eastwards as it is to be westwards for New Zealand–South American events. Sanmartín *et al.* (2007) concluded that only once we have a better understanding of dispersal process will it be possible to apply realistic estimates of dispersal frequency and asymmetry to biogeographical reconstructions. This also seems valid for a better understanding of vicariance processes, which frequently have been oversimplified as a several-steps break-up model, obscuring the complex geological and biotic nature of the southern lands. A composite nature has been documented for Australasia (Morley, 2001), New Zealand (Craw, 1988), the Subantarctic Islands (Michaux & Leschen, 2005), Tasmania (Heads, 1999), New Guinea (Heads, 2002) and South America (Crisci *et al.*, 1991; Katinas *et al.*, 1999).

DECONSTRUCTION OF THE BIOGEOGRAPHICAL CLASSIFICATION

Cox asks whether the concept of floral kingdoms is still useful and necessary (i.e. 'the role of floral kingdoms'). Many authors have in fact called for the deconstruction of the concept of floristic regions, Alphonse de Candolle being one of the first to reject such schemes of regions and to criticise the task of floristic classification: 'Je tiens donc les divisions du globe par régions, proposées jusqu'à présent, pour des systèmes artificiels.... Elles ont nui à la science' (de Candolle, 1855, pp. 1304–1305).

Drude, too, after several attempts finally abandoned his work on floristic classification altogether: 'Die in den *Geographischen Mitteilungen* von 1884 veröffentlichten Karten meiner Florenreichseinteilung zeigen die Unbestimmtheit der Grenzlinien in zahlreichen Wanderungszügen und Ausbreitungsrichtungen, welche von einem zum anderen Florenreich hinüberleiten; längst hat man eingesehen, daß jeder Versuch, starre Grenzlinien festzusetzen, in sich selbst zerfallen muss' (Drude, 1890, p. 329).

Hermann von Ihering wrote in this respect: ‘...this example demonstrates the absurdity of the present system of construction of zoogeographical regions and maps. We can construct maps for the different classes and orders but not at all of the animal kingdom, because the geological history of the different groups is quite different. When Osborn says that it is one problem “to connect living distribution with distribution of past time”, he says only what has been the leading idea of Wallace and of Engler in their eminent works on zoogeography and phytogeography, but when he continues “and to propose a system which will be in harmony with both sets of facts”, he proposes a problem just as contradictory as would be the construction of descriptions and figures referring at the same time to egg, larva, nymph and imago of an insect’ (von Ihering, 1900, p. 864).

Nelson (1978, p. 295) further interpreted one of Croizat’s main principles as follows: ‘the main biogeographical regions for terrestrial organisms are not those of Sclater and Wallace, but regions no one has considered before, because they correspond not to modern continents but rather to modern ocean basins’. This concept was firmly adopted by panbiogeographers (Craw & Page, 1988, p. 180). In Craw *et al.*’s (1999) opinion, the refinement of this concept seems to be the only real possibility for the revival of biogeographical classification. In this sense, some recent authors have abandoned regionalization, preferring to describe the Austral floristic relationship as a South Pacific track, composed of some 50 genera and seven families restricted to southern South America and Australasia (e.g. Crisp *et al.*, 1999).

Earlier attempts to characterize the Austral realm have been rendered outdated by considerable changes in family delimitations

resulting from molecular phylogenetic studies. Nowadays, 15 families can be considered as components of this South Pacific track, as shown in Table 6, as summarized from general (e.g. Stevens, 2001 onwards) and specific (e.g. Dillon & Muñoz-Schick, 1993) sources. Furthermore, 55 genera composing an Austral generalized track are marked in Appendix S1 with an asterisk.

Crisp *et al.* (1999) also listed several closely related generic groups, for example *Drimys/Tasmannia/Pseudowintera* and *Austrotaxus/Pilgerodendron/Libocedrus/Papuacedrus*, that characterize the South Pacific track. We can add Chilean/Argentinian *Aextoxicon* as closely related to *Berberidopsis*, a Chilean/Australian genus (Ronse De Craene, 2004). In addition, *Lebetanthus* (Ericaceae) from Magallanes is closely related to *Prionotes* from Tasmania (Crayn *et al.*, 1998), and the New Zealand genus *Stilbocarpa* (Apiaceae) seems to be closely related to the Patagonian *Huanaca* (Andersson *et al.*, 2006). Furthermore, Vinnersten & Bremer (2001) proposed that the isolation of South America from Australia and New Zealand corresponds to the split of the South American *Lapageria* and *Philesia* (Philesiaceae) from the Australian–New Zealand *Ripogonum*, estimated to have occurred 47 Ma. Finally, the Chilean monotypic endemic Gomortegaceae was shown to form the sister clade to the South Pacific Atherospermataceae by Renner (2004). This author further suggests that *Gomortega* could be a 100-Myr-old relict genus/species.

For the relationship between Central Chile and South Africa, we can also consider the Chilean endemic Francoaceae as being closely related to South African Melianthaceae (Ronse De Craene *et al.*, 2001). Andean endemic Malesherbiaceae are

Table 6 Families composing the Austral floristic realm. Data sources: Stevens (2001 onwards) and references therein*.

Family	Distribution	Genera/species
Araucariaceae	SE Asia, western Pacific, South America (disjunct southern Chile/Argentina and SE Brazil)	3/38
Asteliaceae	New Zealand, Tasmania, SE Australia, New Guinea, Pacific Islands, Hawaii, Chile, Mascarenes	2–4/36
Atherospermataceae	Chile/Argentina, Tasmania, Australia, New Zealand, New Caledonia, New Guinea	6/11
Berberidopsidaceae	Chile, E Australia	1/2
Calceolariaceae	Tropical and W temperate South America, Brazil, New Zealand	2/240–270
Centrolepidaceae	SE Asia, Malesia, New Zealand, southern South America	3/35
Corsiaceae	Southern South America, SE Asia, Papuasia-Australia	3/30
Cunoniaceae (incl. Eucryphiaceae)	Australasia, South Africa, Madagascar, Central and South America	27/280
Escalloniaceae	Central and South America, SE and SW Australia, New Zealand, Réunion Is.	8/68
Griselinaceae	New Zealand (2 spp.), Chile (5), Argentina, Brazil (1)	1/7
Luzuriagaceae	Southern Argentina and Chile, Falkland Islands, New Zealand and Australia (New South Wales to Tasmania)	2/5
Nothofagaceae	New Guinea, New Caledonia, E Australia, New Zealand, South America	1/36
Proteaceae	Australasia, Africa, South America	70/1000
Restionaceae	Australasia, South Africa, Madagascar, South America	58/520
Stylidiaceae = Donatiaceae	South East Asia to New Zealand, southern South America	6/157

*Tetrachondraceae (two genera, three species) has traditionally been considered as a southern family, but the recent inclusion of the genus *Polyprenum* from North and Central America by Wagstaff (2004) does not permit inclusion of the family on this account.

closely related to the American/African Turneraceae (Gengler-Nowak, 2003).

For the relationship between the CFR and Australasia, Crisp *et al.* (1999) and Galley & Linder (2006) further proposed a Trans-Indian Ocean track composed of the sister clades of *Ehrharta*, the *Pentaschistis* clade, the Restionaceae and Geissolomataceae, and several clades in the Proteaceae. The Restionaceae and Proteaceae appear to belong to Gondwanan groups, and they show in the Cape the highest levels of endemism at the generic level (Goldblatt & Manning, 2000). Both families serve to connect the South Pacific and the South Indian tracks, forming together an Antarctic track (Croizat, 1958), or, as noted early on by Hooker (1844–1860), a circumpolar Antarctic flora.

CONSIDERATIONS FOR THE RECONSTRUCTION OF THE AUSTRAL REALM

1. Earlier authors (e.g. Takhtajan, 1986), as correctly noted by Cox (2001), did not solve the problem of the South Pacific disjunct relationships because they incorrectly included several American families, such as Gomortegaceae, Malesherbiaceae, Francoaceae, Aextoxicaceae, into a Holantarctic kingdom. However, in spite of the fact that these families show a strictly American distribution, most of them have phylogenetic relationships with Australasia or South Africa (Ronse De Craene *et al.*, 2001; Gengler-Nowak, 2003; Renner, 2004).

2. Floristic similarity at the genus level shows that southernmost South America (i.e. the Magallanes region) is almost equally similar to northern Chile as it is to New Zealand. In fact, there are more genera shared between NZ and MAG than between MAG and ANT, in spite of the oceanic distance that separates the southern masses. Many of the taxa involved in this relationship show a history that can be traced to the times of Gondwana (e.g. Nothofagaceae, Cunoniaceae, Winteraceae) (Eklund, 2003; Poole *et al.*, 2003).

3. The revival of biogeographical classification has its best possibilities in the continued search for repeated disjunct distribution patterns, for example as in panbiogeographical analysis. There are 15 families and c. 60 genera that, under current taxonomic treatment, support the segregation of an Austral realm, or, in the panbiogeographical terminology, an Austral generalized track.

4. Jaccard's similarity analysis shows that the CFR has a low level of similarity to South America and New Zealand. The Cape Region could therefore be treated as a region of an African kingdom (Cox, 2001), as a proper floristic realm (Diels, 1908), or as a node from a circum-Antarctic track (Croizat, 1958). This controversial issue is still to be tested in a 'less superficial and inconsistent fashion by including some systematic account' (Cox, 2001). Floristic groupings for an assessment of the CFR within South Africa have recently been carried out by Born *et al.* (2007).

5. Contrary to Cox's concern that '...zoologists do not find any similarities between the faunas of the southernmost regions of the world similar to those that have led the botanist

to establish the Antarctic floral region' (Cox, 2001, p. 513), many groups do indeed show transantarctic relationships (Brundin, 1966; Crisci *et al.*, 1991). Recently, the three-realm global biotic scheme of Morrone (2002) found support in the analysis of the Polychaeta (Glasby, 2005). In the opinion of Glasby (2005), biogeographical analysis at the global scale is a major challenge, since: '...global revisions are resource intensive [so much so that they are usually only undertaken by PhD students!], and whilst undeniably comprehensive may in fact represent an over-utilisation of resources' (Glasby, 2005, p. 243). Systematic accounts for faunistic regions at a global scale have been proposed by Smith (1983) and by Procheş (2005).

6. The history of the Austral biota seems to be tied to ancient palaeogeographies that we do not yet fully understand, involving many geological and biogeographical composite areas.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article online

Appendix S1 Genera shared between Chilean regions, New Zealand and the Cape Floristic Region.

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/abs/10.1111/j.1365-2699.2007.01757.x>

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BIOSKETCH

Andrés Moreira-Muñoz has a degree in geography from the Universidad Católica de Chile and recently finished doctoral research in Germany. He is working on the phytogeography of Chilean vascular plants and is interested in plant systematics, conservation, and the history of plant geography.

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