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PHYTOGEOGRAPHICAL AND ECOLOGICAL AFFINITIES OF THE BRYOFLORISTIC REGIONS OF SOUTHERN AFRICA

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Abstract. There is a high degree of correspondence between the bryofloristic regions of southern Africa and phytochoria based on the distribution of seed plants, especially those of White and Linder. The bryofloristic classification provides evidence for a greater Afromontane Region that includes the Cape Floristic as well as the Maputaland-Pondoland Regions, but excludes the Afro-alpine Region. Recent numerical classifications of the region do not support a Greater Cape Floristic Region or Kingdom, but reveal the existence of a broad-scale temperate (Afrotemperate) phytochorion consisting of the Kalahari-Highveld and Karoo-Namib Regions. Endemism is much lower in the moss than the seed plant floras of congruent phytogeographical regions. The bryofloristic regions correspond in varying degrees with the biomes and vegetation types of southern Africa.

Key words: Plant biogeography, floristic region, biome, phytochorion, mosses, TWINSPAN, southern Africa

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INTRODUCTION

Phytogeographical classifications of Africa have generally been based on the distribution of seed plants only. Detailed accounts of the history of these divisions were published by Monod (1957), Werger (1978a), Denys (1979), Friis (1986, 1998) and Iversen (1991). Cowling and Hilton-Taylor (1997) provided a short synopsis for southern Africa. Recent phytogeographical classifications of southern Africa include those of Van Wyk and Smith (2001), Steenkamp *et al*. (2005), Linder *et al.* (2005), and Born *et al.* (2007).

The main objective of this paper is to compare the recently described bryofloristic regions of southern Africa (Van Rooy & Van Wyk 2010) with those proposed for seed plants of the subcontinent, and to test the hypothesis that they correspond. The bryofloristic regions are also compared with ecological classifications of the vegetation.

We also hope to solve some of the problems and controversies in the delimitation of southern African phytochoria, namely the recognition of a central Kalahari-Highveld Region, inclusion of the winter-rainfall part of the Karoo-Namib Region in a Greater Cape Floristic Region or Kingdom, the recognition and affinity of an Afro-alpine Region, and the relationship between the Cape Floristic and Afromontane Regions (Cowling & Hilton-Taylor 1997; Linder *et al*. 2005; Born *et al*. 2007).

MATERIALS AND METHODS

All bryofloristic regions (including main regions, Regions and Domains) delimited by a TWINSPAN classification (Hill 1979) of southern African (South Africa, Botswana, Namibia, Lesotho, Swaziland) moss distribution data (Van Rooy & Van Wyk 2010) were compared with phytogeographical as well as vegetation classifications of the region. The bryofloristic Regions in Figures 1 and 2, overlaid with seed plant regions based mainly on White (1983) and biomes based on Rutherford *et al*. (2006), are derived from a TWINSPAN classification of Van Rooy and Van Wyk's (2010) TWINSPAN 3+

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distribution database, which includes all (295) 0.5° grid squares in which three or more moss species occur.

The percentage moss species diversity and endemism in the bryofloristic regions (Table 1) were calculated from the figures in the TWINSPAN 3+ tables provided by Van Rooy and Van Wyk (2010). Figures for the seed plant phytochoria were obtained from various sources listed in Table 1.

Results and discussion

The two main bryogeographical regions

Phytogeographical classifications based on the distribution of seed plants generally divide Africa into a Cape Floristic Kingdom in the south and a Palaeotropical Kingdom in the rest of sub-Saharan Africa (e.g., Good 1974; Takhtajan 1986; Werger 1978a; Jürgens 1991). However, the recent systems of Cox (2001) and Morrone (2002) no longer recognise a separate Cape Floristic Kingdom. The bryofloristic classifications of Herzog (1926) and Schofield (1992) include almost the whole of southern Africa in their southern division, the South African Kingdom.

The primary southern African bryofloristic division of Van Rooy and Van Wyk (2010) seems to correspond to the biogeographical scheme of Morrone (2002). The main subtropical bryofloristic region, consisting of the Zambezian and Afromontane Regions, falls in Morrone's (2002) Afrotropical region, which forms part of his Holotropical kingdom, while the main temperate bryofloristic region, which consists of the Karoo-Namib and Highlands Regions, largely coincides with his Cape or Afrotemperate region of the Austral kingdom. The austral nature of the Cape bryophyte flora was also stressed by Miller (1982).

Zambezian region

The Zambezian bryofloristic Region overlaps with the southern section of White's (1976, 1983) Zambezian Regional Centre of Endemism (Fig. 1). The northeastern region of KwaZulu-Natal (and eastern Swaziland) is biogeographically complex (Van Rensburg *et al*. 2000 and references therein) but the bryofloristic classification based on Van Rooy and Van Wyk's (2010) TWINSPAN 5+ distribution dataset supports the inclusion of this area in the Zambezian Region.

Mosses of the Zambezian Region are associated with woodland or savanna vegetation (Van Rooy & Van Wyk 2010) and this region therefore largely coincides with the Savanna Biome of Low and Rebelo (1996), Rutherford (1997) and Mucina and Rutherford (2006), and the Temperate Xerophytic Woods/Scrub biome of Olson *et al.* (1983) (Fig. 2).

Table 1. Endemism in the bryofloristic regions of Van Rooy and Van Wyk (2010). Species richness and endemism in the moss and corresponding seed plant floras of the bryofloristic Regions and selected Domains of southern Africa.

Bryogeographical regions (this paper)	Mosses		Seed plants		
	% of total moss flora	% endemism	% of total seed plant flora	% endemism	Sources
Zambezian Region	27	1	low 36	low 54	Southern (Goldblatt 1978) Greater (White 1983)
Afromontane Region	96	10	10 23	75 26	White 1983 Maputa-Pondo (Van Wyk & Smith 2001)
Drakensberg Domain	81	7	23	26	Maputa-Pondo (Van Wyk & Smith 2001)
Cape Domain	57	7	27	70	Van Wyk & Smith 2001
Karoo-Namib Region	39	6	17	40	Van Wyk & Smith 2001
Western Cape Domain	38	6	20	40	Hilton-Taylor 1996
Highlands Region	30	1	13	low	Kalahari-Highveld (White 1983)
Drakensberg Alpine Domain	28	1	13	16	Carbutt & Edwards 2004, 2006

CAPRIVI AND BUSHVELD DOMAINS

Whether the two subdivisions of the already discontinuous Zambezian bryofloristic region (see Van Rooy & Van Wyk 2010) coincide with any of the seed plant divisions reviewed by Werger and Coetzee (1978), or represent artefacts of insufficient data, remains to be investigated further. Another possibility is that the Caprivi bryofloristic Domain represents the Guinea-Congolia/Zambezia Transition Region, and the Bushveld Domain the Zambezian Region, both of Denys (1980).

AFROMONTANE REGION

This bryofloristic region largely coincides with White's (1978) southernmost division of the Afromontane archipelago-like regional centre of endemism, the Drakensberg regional mountain system, especially if the Magaliesberg extension and other satellite populations and transition zones are included (Fig. 1), as well as the Drakensberg Domain of Denys (1980), which includes two substantial islands in the southern and southwestern Cape. A separate Maputaland-Pondoland Region (Moll & White 1978; Van Wyk & Smith 2001) was not retrieved at the first three levels of the bryofloristic classification, corroborating the results of Steenkamp *et al*. (2005) and Linder *et al*. (2005) who incorporated the Maputaland-Pondoland Region in their Greater Afromontane and Natal phytochoria respectively. The bryogeographical region also corresponds to the South African Centre of *Kniphofia* diversity, regarded as a floristic indicator of the broader Afromontane Region (Ramdhani *et al*. 2008).

The bryofloristic classification lends support to a combined Cape-Afromontane phytogeographical region as recognised by Linder (1990, 1994), Oliver (1994) and Galley *et al*. (2007). However, the bryofloristic region is not of temperate, but of subtropical affinity and excludes high altitude (Highlands) areas such as the Lesotho plateau, known as the Afro-alpine Region.

Although it has been suggested that the two main zonal forests in southern Africa belong to different phytogeographical regions (Cawe *et al*. 1994; Mucina & Geldenhuys 2006), bryofloristically all forests in the region, whether they occur in the Savanna, Grassland, Albany Thicket or Fynbos Biome (Fig. 2), are indicators of the Afromontane Region.

DRAKENSBERG DOMAIN

The northern subdivision of the Afromontane Region is named after the Drakensberg Domain of Denys (1980). The bryofloristic Domain delimited by the TWINSPAN classification of Van Rooy and Van Wyk's TWINSPAN 3+ dataset (TWINSPAN 3+ domain) coincides with the Natal phytochorion of Linder *et al.* (2005), but we regard it as a greater Afromontane Region (Steenkamp *et al*. 2005) rather than an expanded Maputaland-Pondoland Region. The TWINSPAN 5+ domain (Van Rooy & Van Wyk 2010), which extends further west than the TWINSPAN 3+ domain, is similar to the Drakensberg regional mountain system of White (1978).

CAPE DOMAIN

The remarkable diversity, endemism and composition of the seed plant flora of the southwestern Cape have contributed greatly to the recognition of this area as one of the phytogeographical Kingdoms of the world (Werger 1978a; Takhtajan 1986; Cowling & Richardson 1995; Goldblatt & Manning 2000). However, the Cape phytochorion based on the distribution of southern African mosses is rather less distinctive and only separated at the level of Domain. Others in favour of a lower rank for the Cape phytochorion include Hilliard and Burtt (1987) and Linder (1990, 1994), who demonstrated close links with the Afromontane Region. More recently, Cox (2001) argued that the Cape only warrants recognition at the level of Province rather than Region or Kingdom. He proposed a revised system of Takhtajan's (1986) floral Kingdoms in which the Cape, accepted at the level of Region, is incorporated into the African Kingdom.

The Cape Domain is more or less restricted to the mountains of the Cape Fold Belt, covered by the Afromontane Forest and Mountain Fynbos vegetation types of Campbell (1985) and Low and Rebelo (1996), or the different Fynbos Bioregions of Mucina and Rutherford (2006).

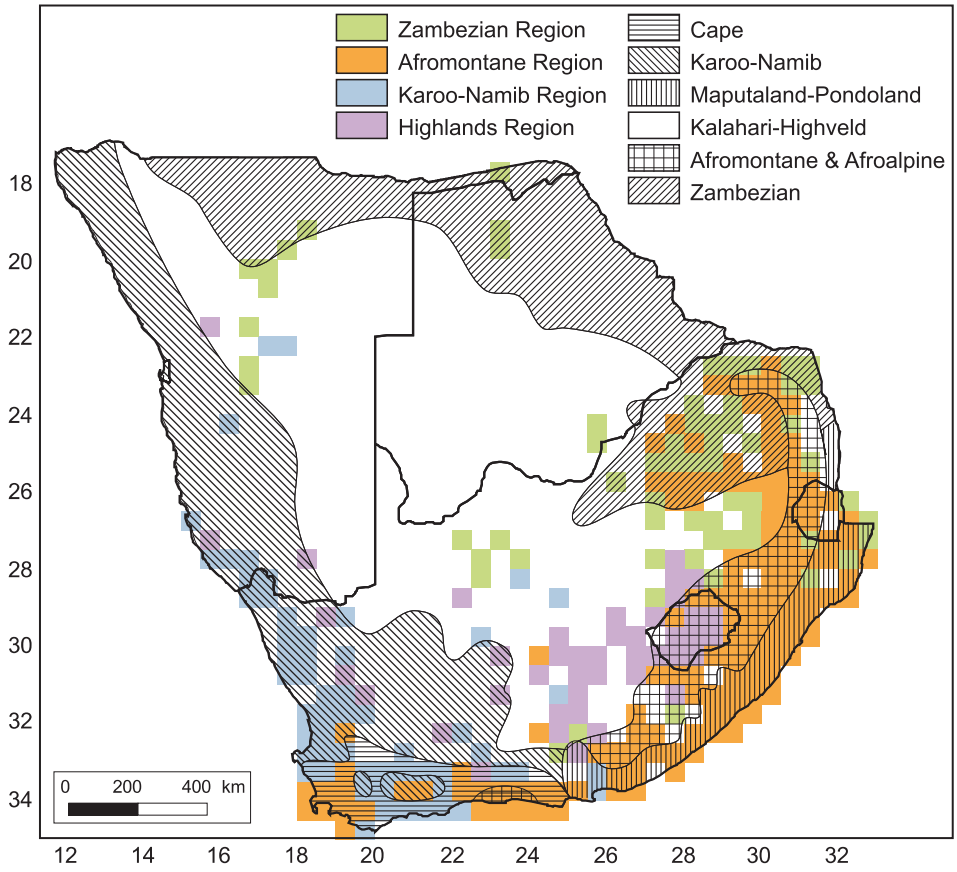

Fig. 1. The phytogeographical regions of southern Africa, based mainly on White (1983), with modifications from Huxley *et al.* (1998), superimposed on the bryofloristic regions of Van Rooy and Van Wyk (2010). Map redrawn from Van Wyk and Smith (2001).

The bryofloristic domain is largely congruent with the Capensis of Werger (1978a) and the Cape phytochoria of White (1983), Goldblatt (1978) and Linder *et al*. (2005).

KAROO-NAMIB REGION

The bryofloristic region is similar to the Karoo-Namib Region of White (1976, 1983) and Takhtajan (1986), the Succulent Karoo Region of Van Wyk and Smith (2001), and the Namib-Karoo phytochorion of Linder *et al*. (2005) (Fig.1). The eastern boundary is unresolved but at present the bryofloristic region is narrower than the Karoo-Namib Region of Werger (1978b).

The northern boundary of the bryofloristic region coincides with the boundary between the Succulent Karoo and Desert Ecozones (Biomes) of McCullum (1994) and Rutherford (1997). However, the outliers in central Namibia may indicate that this bryogeographical region extends northwards, to coincide with the phytochoria of Werger (1978a) and White (1983). The eastern boundary of the Karoo-Namib Region runs parallel to the Atlantic coastline, following the Great Escarpment for most of the way, and coincides with the boundary between the Succulent Karoo and Nama-Karoo Ecozones (Biomes) of McCullum (1994), Rutherford (1997) and Mucina and Rutherford (2006) (Fig. 2). In the south the Karoo-Namib Region borders on

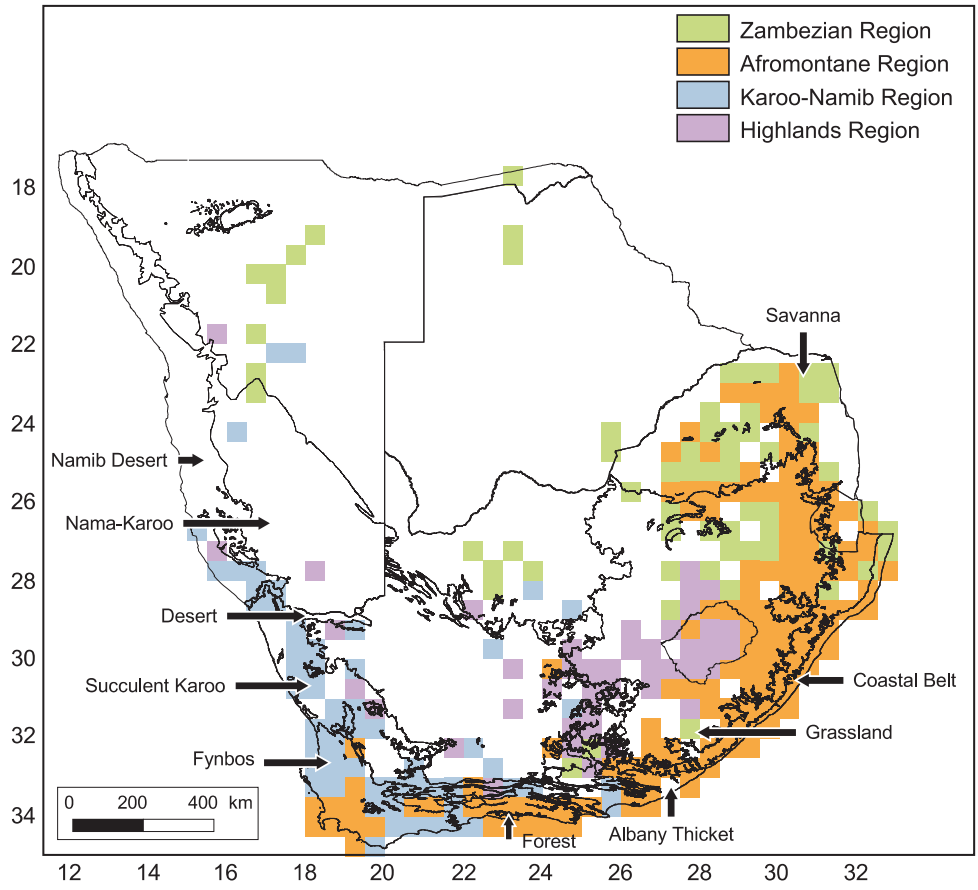

Fig. 2. The biomes of southern Africa after Rutherford *et al*. (2006), superimposed on the bryofloristic regions of Van Rooy and Van Wyk (2010).

the Fynbos Biome of Rutherford (1997) and Mucina and Rutherford (2006) (Fig. 2).

The bryofloristic classification confirms that the karroid shrublands of the Robertson as well as the Little Karoo belong to the Karoo-Namib Region (White 1983; Van Wyk & Smith 2001; Mucina *et al*. 2006).

WESTERN CAPE AND NAMAQUA DOMAINS

More distribution data are needed to critically compare the bryofloristic and seed plant subdivisions of the Karoo-Namib Region, but at this stage it appears that the Western Cape Domain partly coincides with the Succulent Karoo Regions of Jürgens (1991) and Van Wyk and Smith (2001), and the Western Cape Domain of Hilton-Taylor (1994). It also overlaps with the Succulent Karoo Biome of Hilton-Taylor (1996), Milton *et al*. (1997), Rutherford (1997) and Mucina and Rutherford (2006).

Although the boundaries of the Namaqua Domain are poorly defined as a result of insufficient sampling, the TWINSPAN 3+ domain of Van Rooy and Van Wyk (2010) appears to coincide with, and is therefore named after, the Namaqualand (Namaland) phytochorion of Monod (1957), Werger (1978a, 1978b), Takhtajan (1986) and Jürgens (1991). In the TWINSPAN 5+ classification the bryofloristic domain has shifted northwards to overlap with the Namib-Desert Region of Born

et al. (2007), the Gariep Centre of Van Wyk and Smith (2001), and the Northern Succulent Karoo phytochorion of Steenkamp *et al*. (2005).

HIGHLANDS REGION

At present this bryogeographic region is very much restricted to the Highlands of Lesotho and adjacent interior plateau, including the Afro-alpine or Drakensberg Alpine Region of Killick (1978, 1994), and largely coincides with the Eastern Karoo phytochorion of Linder *et al*. (2005). However, a separate Kalahari phytochorion as delimited by Linder *et al*. (2005) was not retrieved by the bryofloristic classification, which may be due to undersampling (Van Rooy & Van Wyk 2010), or the presence of a broader Kalahari-Highveld transition zone or Region as suggested by White (1976, 1983), and adopted by Goldblatt (1978), Cowling and Hilton-Taylor (1997) and Van Wyk and Smith (2001) (Fig. 1).

The Highlands bryofloristic Region also overlaps with Udvardy's (1975) South African Highlands Province, which covers the high altitude plateau along the eastern escarpment of South Africa and forms part of his archipelago-like African Highlands region. However, if the main temperate (Afrotemperate) region of southern Africa, represented by the Karoo-Namib and Highlands bryofloristic Regions, is sufficiently distinct from other temperate areas in Africa, its proper relationship may indeed lie with other southern temperate areas of the world to form a separate Austral kingdom, as proposed by Morrone (2002).

The Highlands Region falls in the Grassland Biome as delimited by Mucina and Rutherford (2006), with substantial outliers in the adjacent Nama-Karoo Biome (Fig. 2), and occupies more or less the same geographical area as the Steppe biome of Olson *et al*. (1983).

DRAKENSBERG ALPINE AND UPPER KAROO DOMAINS

The recognition of a separate Afro-alpine Region is one of the controversies in southern African phytogeography (Killick 1978; Cowling & Hilton-Taylor 1997). The existence of a distinct, discontinuous Afro-alpine Region has generally been acknowledged, but often as a subdivision or 'impoverished' part of the Afromontane Region (White 1978, 1981, 1983; Goldblatt 1978; Denys 1980; Cowling & Hilton-Taylor 1997; Steenkamp *et al*. 2005).

However, Lovett (1993) found evidence in the mountains of eastern Tanzania that the Afro-alpine (vegetation) belt is temperate in origin while the Montane forest belt is tropical. He suggested that the two belts be placed in separate phytogeographical regions, with the Afro-alpine and Ericaceous belts in an Afro-alpine region. Grimshaw (2001) supported this view and proposed that the Afro-alpine and Ericaceous belts be treated as a single entity called the altimontane belt. After analysing data presented by Hilliard and Burtt (1987), Grimshaw (2001) suggested that 'it may eventually be appropriate therefore to regard the southern African alpine flora as a sub-region of an African Altimontane Region, designated by the prefix Austro-'.

The Drakensberg Alpine Domain of Van Rooy and Van Wyk (2010) is largely congruent with, and is named after, the Afro-alpine or Drakensberg Alpine Region (Centre) of Killick (1978, 1994), Van Wyk and Smith (2001) and Carbutt and Edwards (2004, 2006). It also largely coincides with the Austral Domain (Afro-alpine Region) of Werger (1978a) and the Eastern Mountain Region of Phillips (1917), renamed the South-eastern Mountain Regional Mosaic by Hilliard and Burtt (1987). However, the boundaries of the seed plant regions were artificially drawn, resulting in the inclusion of subtropical Afromontane forest elements on the KwaZulu-Natal side of the Drakensberg escarpment.

The Drakensberg Alpine Domain is largely congruent with the Drakensberg Grassland Bioregion of Mucina and Rutherford (2006), which includes heathlands similar to those on the East African mountains, Madagascar and the Mascarenes. The other Highlands bryofloristic subdivision, the Upper Karoo Domain, corresponds with the Dry and Mesic Highveld Grassland Bioregions of Mucina and Rutherford (2006) with outliers in the Upper Karoo Bioregion.

ENDEMISM

A relatively high percentage of southern African mosses occur in each bryofloristic region but endemism is much lower compared to that of the seed plant floras (Table 1). Moss endemism in the Karoo-Namib Region, in particular the Western Cape Domain, is expected to increase as a result of recent discoveries (Van Rooy & Van Wyk 2010). Endemism is extremely low or absent in the moss as well as the seed plant floras of the Highlands (Kalahari-Highveld) Region (Table 1). However, Goldblatt (1978) and White (1983) excluded the Drakensberg (Afro-) Alpine flora from their Kalahari-Highveld Region. Endemism may also be higher in the moss flora of this region as a result of the course grain chosen for the bryofloristic classification (Van Rooy & Van Wyk 2010).

CONCLUSIONS

There is a high degree of correspondence between the bryofloristic regions of Van Rooy and Van Wyk (2010) and southern African phytochoria based on the distribution of seed plants, especially the regions of White (1976, 1983), adopted with modifications by others like Goldblatt (1978), Cowling and Hilton-Taylor (1997) and Van Wyk and Smith (2001), and the southern African phytochoria of Linder *et al*. (2005), retrieved by a numerical analysis of selected African plant distributions. Major deviations from White's classification are the delimitation of a greater Afromontane Region and the affinity of the Afro-alpine Region. The main discrepancies between the bryofloristic regions and the phytochoria of Linder *et al*. (2005) lie in the recognition of an Afromontane Region, the level at which the Cape phytochorion is recognised, and the delimitation of the central Highlands or Kalahari-Highveld Region.

The bryofloristic classification supports the recent tendency towards a greater Afromontane Region that includes the Cape Floristic as well as the Maputaland-Pondoland Regions, but excludes the high altitude Afro-alpine Region of the interior highlands, which is a distinct temperate phytochorion. Although a separate Cape bryofloristic phytochorion was only retrieved at a lower level, the inclusion of seed plant distributions may render it distinct at the regional level, as was found by Linder *et al*. (2005). The northern Afromontane subdivision (Drakensberg Domain) is here regarded as expanded Afromontane rather than expanded Maputaland-Pondoland (Van Wyk 1994; Van Wyk & Smith 2001; Linder *et al*. 2005).

A Greater Cape Floristic Region or Kingdom, as proposed by Jürgens (1991), Steenkamp *et al*. (2005), Born *et al*. (2007) and Snijman *et al*. (2008), is not supported by the bryofloristic scheme as it includes winter-rainfall areas on both sides of the main bryofloristic division line (Van Rooy & Van Wyk 2010) as well as such diverse vegetation types as Lowland Succulent Karoo and Mountain Fynbos. This is also in agreement with Linder *et al*. (2005) who found that their Cape phytochorion is closer related to the mesic Afromontane Region (their Natal) than the xeric Succulent Karoo Region.

The recent phytogeographical analyses of Linder *et al*. (2005) and Van Rooy and Van Wyk (2010) revealed a broad-scale, temperate phytochorion, consisting of the Kalahari-Highveld and Karoo-Namib Regions in the central and western parts of southern Africa. This Afrotemperate phytochorion supports Morrone's (2002) hypothesis of a Cape or Afrotemperate biogeographical region (belonging to his Austral kingdom) in the southern part of Africa, and should not be confused with the Afrotemperate region of Linder (1990) and Galley *et al*. (2007), which combines the Afromontane and Cape phytochoria of White (1983).

It is generally accepted that the greater dispersability of diaspores and greater age of bryophytes result in wider distribution ranges and lower endemism compared to seed plants (Pócs 1998 and references therein). This is also true for southern Africa where endemism is much lower in the moss than the seed plant floras of congruent phytogeographical regions.

Although the large unresolved areas in the arid and semi-arid regions of the subcontinent hamper direct comparison with vegetation zones, the bryofloristic regions follow the general trend in southern African phytogeography (Rutherford

et al. 2006) by corresponding in varying degrees with the biomes and vegetation types of the region.

We believe that an objective numerical analysis of the geographical distributions of all indigenous plant species will go a long way in resolving the remaining controversies in the delimitation of southern African phytochoria.

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