THE BRYOFLORISTIC REGIONS OF SOUTHERN AFRICA

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SUMMARY

A TWINSPAN classification divides southern Africa (South Africa, Namibia, Botswana, Swaziland and Lesotho) into two main bryofloristic regions: (1) a subtropical or palaeotropical region in the northern, eastern and southern parts, characterised by a predominantly mesophytic moss flora, and (2) a temperate or austral region in the central and western parts of the study area with a xerophytic moss flora. The subtropical region is subdivided into the Zambezian and Afromontane Regions, and the temperate region into the Karoo-Namib and Highlands Regions. The four regions are further subdivided into eight domains: (1) the Zambezian Region into the Caprivi and Bushveld Domains, (2) the Afromontane Region into the Drakensberg and Cape Domains, (3) the Karoo-Namib Region into the Western Cape and Namaqua Domains, and (4) the Highlands Region into the Drakensberg Alpine and Upper Karoo Domains. Meaningful phytogeographical classification of the arid and semi-arid central and northwestern sectors of the study area is dependant on future plant collecting or sampling efforts.

KEYWORDS: Distribution patterns, floristic regions, moss flora, numerical classification, TWINSPAN, plant biogeography, southern Africa.

INTRODUCTION

The two main concepts in descriptive or floristic plant geography are the floristic region, and the floristic element (Birks, 1987; Myklestad & Birks, 1993; McLaughlin, 1994). A floristic region, also known as a phytogeographical region, consists of geographical areas of similar floristic composition while a floristic element consists of plant taxa (e.g. species) of similar geographical distribution. Floristic regions cannot overlap geographically but they may share a number of taxa. A floristic region of any rank is also known as a phytochorion. A floristic region should not be confused with a centre of plant diversity or endemism (see Van Rooy, 2000; Procheş, 2005) which is a geographical area with a high concentration of plant taxa or endemics.

Although the taxonomy of tropical bryophytes, in particular tropical African bryophytes, has generally lagged behind that of northern temperate regions (Touw, 1974; Argent, 1979; Richards, 1984; Churchill, Griffin III & Lewis, 1995; O'Shea, 1997, 2005), considerable progress has been made in southern Africa (Buck & Thiers, 1989; Van Rooy, 2000; O'Shea, 2005). However, until recently (Van Rooy, 2000) a detailed analysis of the diversity, endemism and distribution patterns of southern African mosses was lacking.

The main objective of this paper is to delimit and describe bryofloristic regions in southern Africa by means of a repeatable, numerical technique. This classification will hopefully contribute towards a new bryogeographical classification of the world, as proposed by Ochi (1973), Lewis (1990) and Schofield (1992).

MATERIALS AND METHODS

Study area

The study area occupies the southern tip of the African continent, or Africa south of the Kunene, Okavango and Limpopo Rivers (Fig. 1). Known as the Flora of Southern Africa (FSA) region, it comprises the countries of South Africa, Namibia, Botswana, Swaziland and Lesotho, an area of c.2.7 million km² (Cowling, Richardson & Pierce, 1997). The Indian Ocean forms the boundary on the eastern and southern sides while the Atlantic Ocean runs along the west coast. The northern boundary is not entirely natural (Werger, 1978b) and follows political boundaries between countries.

The southern African land-mass achieved its present general outline during the break-up of Gondwana (Moon & Dardis, 1988). Today the subcontinent is characterised by a high interior plateau, bounded on three sides by the Great Escarpment (Partridge & Maud, 1987). The plateau is tilted to the west and consists of elevated mountain massifs like the Lesotho Highlands, exceeding 3000 m in places, and large basins such as the Kalahari and Transvaal Bushveld. The escarpment comprises a number of distinct mountain ranges such as the Joubert's, Erongo and Naukluft in Namibia, the Kamiesberg of Namaqualand, the Roggeveld and Nuweveld of the Karoo, and the Drakensberg of KwaZulu-Natal, Mpumalanga and Limpopo. Below the escarpment lies the coastal plain or Marginal Zone, 50 to 200 km wide, in places deeply dissected by river gorges. The Cape Fold Belt mountains in the southwestern corner of the subcontinent provide for the highest altitudes in this zone.

Data sets

All 503 southern African moss species and infraspecific taxa accepted by Van Rooy (2000) were included in the TWINSPAN Complete data set. Fortunately only two species, the FSA endemics *Plaubelia involuta* (Pottiaceae) and *Pseudoleskeopsis unilateralis* (Leskeaceae), were lost when outliers (species poor grids) were deleted for the TWINSPAN 3+ and 5+ data sets (see Van Rooy 2000).

We chose ½° grid squares (Edwards & Leistner, 1971) in order to keep the data sets manageable and to reduce the effect of sampling (collecting) bias. In total 1036, ½° grid squares were selected to cover the entire FSA area, of which only 416, or 40% of the total number of grids, contained records of mosses (see map in Van Rooy, 2000). Geographical distribution data was recorded directly from specimen labels in PRE (incorporating specimens from NH, Compton ex SAMH, and STE on permanent loan), specimens in other southern African herbaria (Magill, 1980), type specimens received on loan, as well as literature records based on herbarium specimens (see Van Rooy, 2000).

The presence/absence data matrix of the TWINSPAN 3+ data set therefore consists of 501 species/infraspecific taxa and 298 grids in which three or more species/infraspecific taxa have been recorded. The TWINSPAN 5+ data set consists of 501 species/infraspecific taxa and 252 grids with five or more species/infraspecific taxa recorded.

Data analysis

The moss distribution data sets were subjected to classification by the computer program TWINSPAN (Hill, 1979), a divisive, hierarchical classification technique that detects overall patterns of differences in biological data. Gauch & Whittaker (1981) found that certain advantages "make TWINSPAN the best general purpose method, especially when a data set is complex, noisy, large or unfamiliar", as with the moss distribution data sets used in this study. Default settings were used for all TWINSPAN parameters.

Bryofloristic classification

The bryofloristic classification is hierarchical and based exclusively on the results of the TWINSPAN 3+ and 5+ analyses. The International Code of Area Nomenclature (ICAN), an attempt to improve communication among biogeographers (Ebach *et al*. 2008), suggests the following principal ranks, in descending order, for biogeographical areas: realm, region, dominion, province and district. However, we have chosen the formal ranks of region and domain for the bryofloristic areas at the 2nd and 3rd levels of TWINSPAN division.

RESULTS

The first and major TWINSPAN 3+ and 5+ division splits the grid squares into two main groups (Figs 1 & 2 in the Supplementary Information): region 1/1 (1st level of division, group 1) and region 1/2 (1st level of division, group 2). The two main groups

are subdivided into four groups at the second level (2/1–2/4), and eight groups at the third level of division (3/1–3/8). TWINSPAN goes on to classify the TWINSPAN 3+ and 5+ grid squares into 45 and 39 end groups respectively. However, it is at the second and third levels of division that the groups or regions are comparable with phytochoria at the macroregional scale. These bryofloristic regions are described in detail below. The floristic diversity and endemism of the phytochoria are summarised in Van Rooy (2000).

DESCRIPTION OF THE BRYOFLORISTIC REGIONS AND DOMAINS OF SOUTHERN AFRICA

Zambezian Region (2/1)

Area. In southern Africa the Zambezian Region is at present most continuous in the bushveld (savanna) of Limpopo with disjunctions in the Northern Cape, Eastern Cape, northern Botswana and Namibia (Figs 4 & 5). It consists of 39 TWINSPAN 5+ grid squares, largely discontiguous because of the many empty grids in the northern parts of the study area (Fig. 5). Significant outliers include grids 3030 B (Mkomazi River on the KwaZulu-Natal South Coast), 3224 D (Jansenville in the Eastern Cape), and 2722 A, 2722 D, & 2822 B (Langberge in the Northern Cape), areas known to contain Bushveld or Thicket vegetation types of the Savanna Biome (Rutherford & Westfall, 1986; Low & Rebelo, 1996).

Several aspects of the congruent and similarly named seed plant phytochorion have been described by White (1965, 1983, 1993), Werger & Coetzee (1978),

Goldblatt (1978), Denys (1980), Beentje, Adams & Davis (1994) and Cowling & Hilton-Taylor (1997).

Composition of the moss flora. The moss flora of the Zambezian Region consists of 136 species/infraspecific taxa (27% of mosses in southern Africa) in 74 genera and 31 families, which makes it the smallest of the regional floras (see Appendix 1 in Supplementary Information). The largest family in this region is Bryaceae with 21 species in seven genera. The second and third largest families are Pottiaceae with 17 species/infraspecific taxa in 10 genera and Dicranaceae with 15 species in five genera. *Fissidens* (Fissidentaceae) with 13 species, *Bryum* (Bryaceae) with 12 species and *Campylopus* (Dicranaceae) with 11 species are the largest moss genera in the Zambezian Region.

Characteristic of this flora is the prominence of woodland taxa in the families Bryaceae, Dicranaceae, Erpodiaceae, Fissidentaceae, Meteoriaceae, Pottiaceae and Ptychomitriaceae. Of the diagnostic species (species restricted to this region in southern Africa), only *Fissidens capriviensis* is a true endemic (restricted to the FSA area as well as this region) while *Calymperes tenerum* (Calymperaceae) is pantropical in distribution and *Erpodium grossirete* (Erpodiaceae) ranges northward as far as northeastern Zimbabwe. Other important species (species largely confined to this region in southern Africa), also called near-endemic elements by White (1993), include *Archidium acanthophyllum, Barbula eubryum, Erpodium coronatum* subsp. *transvaaliense* and *Ptychomitrium exaratifolium*.

In addition to the diagnostic and important species, the woodland moss flora also includes more wide-ranging taxa like *Aulacopilum trichophyllum, Bryum capillare, Calymperes pallidum, Erpodium beccarii, Fabronia pilifera, Fissidens*

erosulus, *Octoblepharum albidum*, *Pseudocrossidium porphyreoneurum*, *P. replicatum* and *Syntrichia pagorum*.

Species of the Eastern Highlands and Afromontane Grassland Elements (distribution patterns) are most abundant in this region but none of the bryogeographical elements has its main centre of distribution in the Zambezian Region (Van Rooy, 2000). As could be expected, species of the Cape Element are relatively scarce.

Caprivi Domain (3/1)

Area. This domain consists of a few grid squares in northern Namibia (TWINSPAN 3+ only), the Caprivi and Okavango swamps of northern Botswana, and Limpopo of South Africa (Figs 6 & 7).

Composition of the moss flora. Only 22 mosses (4% of southern African mosses), belonging to 15 genera and 12 families, make up the flora of the Caprivi Domain, most of which belong to the acrocarpous orders of Dicranales, Pottiales and Bryales (Appendix 1 in Supplementary Information). The orders Andreaeales, Funariales, Hookeriales, Hypnobryales and Polytrichales were not recorded from this domain.

The largest moss families are Dicranaceae, Pottiaceae and Bartramiaceae with three species each while *Campylopus* (Dicranaceae) and *Philonotis* (Bartramiaceae) with three species each, and *Fissidens* (Fissidentaceae), *Archidium* (Archidiaceae) and *Erpodium* (Erpodiaceae) with two species each, are the best represented among the genera of this domain.

Diagnostic families and genera are absent. Of the two diagnostic species, *Fissidens capriviensis* is endemic, and *Erpodium grossirete* restricted to this domain in southern Africa. Both are woodland species growing on the bark of trees.

The moss flora of the Caprivi Domain consists mostly of species in the Disjunct Cape Peninsula Subelement while species of the West Coast and Boland Subelements are absent from this area (Van Rooy, 2000).

Bushveld Domain (3/2)

Area. The Bushveld Domain is the largest of the two Zambezian divisions, distributed over 35 savanna grids in Namibia and the northern provinces of South Africa (Fig. 7). In South Africa this domain surrounds the northern part of the Drakensberg Domain (Afromontane Region).

Composition of the moss flora. The moss flora of the Bushveld Domain is essentially the same as that of the Zambezian Region (minus *Aerobryopsis capensis, Brachymenium systylium, Campylopus flaccidus, Erpodium grossirete, Fissidens capriviensis* and *Octoblepharum albidum*). *Octoblepharum* is the only genus in the flora of the Zambezian Region not shared by the Bushveld Domain. The Bushveld moss flora consists of 130 species/infraspecific taxa, representing 73 genera and 30 families (Appendix 1 in Supplementary Information). The most diverse families are Bryaceae with 20 species in seven genera, Pottiaceae with 17 species in 10 genera and Dicranaceae with 14 species in five genera. *Fissidens* (Fissidentaceae) and *Bryum* (Bryaceae) with 12 species each, *Campylopus* (Dicranaceae) with 10 species, and *Philonotis* (Bartramiaceae) with four species are the largest genera in this domain.

Calymperes tenerum (Calymperaceae) is the only diagnostic species (restricted to this domain in southern Africa) but *Archidium acanthophyllum* (Archidiaceae), *Barbula eubryum* (Pottiaceae) and *Ptychomitrium exaratifolium* (Ptychomitriaceae) are also important woodland taxa largely restricted to this domain. At the time of the numerical analysis the Bushveld Domain lacked endemic moss taxa.

The Bushveld Domain is dominated by woodland mosses in the Widespread as well as the Disjunct Cape Peninsula Subelements (Van Rooy, 2000).

Afromontane Region (2/2)

Area. The Afromontane Region is by far the largest of the four bryogeographical regions (Fig. 5). In the northern provinces of South Africa it runs along the Soutpansberg, Drakensberg and Magaliesberg mountain ranges, with an outlier in the Waterberg of Limpopo. It continues south along the Great Escarpment and fans out in KwaZulu-Natal, where it is most prominent, reaching the Indian Ocean in the vicinity of Lake St. Lucia on the Zululand coast. In KwaZulu-Natal and the Eastern Cape the Afromontane Region occupies the Marginal Zone, more or less from the upper margin of the forests down to the Indian Ocean. Near Port Elizabeth on the Eastern Cape coast this region is interrupted by a dry corridor along the Sundays and Great Fish River valleys (Cowling, 1983) before it continues down the coast to the vicinity of Groot Brakrivier. In the southwestern Cape the Afromontane Region is more or less restricted to the forest and mountain fynbos vegetation of the Cape Fold Belt, as far west as Table Mountain in the Cape Peninsula and, in the TWINSPAN 3+ classification, north to the Cederberg (Fig. 4). The southern part of this region is therefore broken up into a series of Afromontane ‘islands’ or ‘archipelagos’,

surrounded by the Karoo-Namib Region along the drier intermontane river valleys and other low-lying areas.

The seed plant vegetation of this region "is characterised by a recurring pattern of forest 'islands' in a 'sea' of grassland or heathland" (Meadows & Linder, 1993). In general it can therefore be said that all areas with indigenous forest, large or small, belong to the Afromontane (bryofloristic) Region. Useful reviews and summaries of the seed plant phytochorion were written by Goldblatt (1978), White (1983, 1993), Meadows & Linder (1993), Beentje *et al*. (1994) and Cowling & Hilton-Taylor (1997).

Composition of the moss flora. The Afromontane Region has the largest and most diverse moss flora of the four bryogeographical regions. The flora consists of 481 species/infraspecific taxa (96% of the total moss flora) in 197 genera and 54 families (Appendix 1 in Supplementary Information). The largest Afromontane moss families are Pottiaceae with 61 species/infraspecific taxa in 24 genera, Dicranaceae with 48 species\infraspecific taxa in 14 genera and Bryaceae with 40 species in nine genera. These families are also the largest in the southern African moss flora. *Fissidens* (Fissidentaceae) with 28 species, *Bryum* (Bryaceae) and *Campylopus* (Dicranaceae) with 19 species each and *Funaria* (Funariaceae) with 10 species are the most species-rich genera in this region.

Characteristic of the Afromontane moss flora is the abundance of pleurocarpous mosses belonging to the Orders Hookeriales, Hypnobryales, Isobryales and Thuidiales. Most species in these groups occur in the forests, forest patches and wooded kloofs (White, 1978, 1983; Midgley *et al*., 1997; Mucina & Geldenhuys, 2006) that give the Afromontane region it's unique character. Although forests and

forest patches represent a small area of this region, at least 48% of Afromontane mosses occur in this biome (Van Rooy, 2000). It is generally accepted that mesic environments favour mosses with a pleurocarpous growth form (Vitt 1979, 1984; Buck & Vitt, 1986).

None of the moss families in southern Africa is endemic to any of the bryogeographical regions. The only moss family endemic to southern Africa, the monotypic Wardiaceae, is found in both the Afromontane and the Karoo-Namib Regions but is largely restricted to the Afromontane Region. The following 11 families (phylogenetically arranged) are diagnostic for the Afromontane Region (restricted to this region in southern Africa) : Seligeriaceae (Dicranales), Splachnaceae (Funariales), Eustichiaceae (Bryales), Rhachitheciaceae and Rhabdoweisiaceae (Orthotricales), Fontinalaceae, Cryphaeaceae, Prionodontaceae, Trachypodaceae and Pterobryaceae (Isobryales), and Rigodiaceae (Thuidiales). The Isobryales is the best represented at the family level with five of its 12 families diagnostic for the region.

The 70 moss genera (34% of the total number of moss genera in southern Africa) which are diagnostic for the region are listed in Appendix 2 of the Supplementary Information. Prominent among the orders, with regard to the number of diagnostic genera, are the Isobryales (13 or 48% of genera in this order), Hookeriales (5 or 63%), Thuidiales (11 or 55%) and Hypnobryales (14 or 48%). The families Ditrichaceae (4), Pottiaceae (4), Pterobryaceae (5), Hookeriaceae (5), Amblystegiaceae (5) and Hypnaceae (4) are the best represented as far as the number of diagnostic genera is concerned.

Physcomitrellopsis of the family Funariaceae and *Quathlamba* of the Bartramiaceae are the only endemic genera. At a finer scale of analysis *Quathlamba* will probably prove to be endemic to the Drakensberg Alpine Domain of the Highlands

Region (see below) while *Wardia* of the monotypic and endemic family Wardiaceae, now shared with the Karoo Namib Region, may actually be endemic to the Afromontane Region.

A total of 188 species/infraspecific taxa, or 39% of species in the Afromontane Region, are diagnostic for the southern African section of the region (Appendix 3 in Supplementary Information). Some of the more widespread diagnostic species are: *Callicostella tristis, Cyclodictyon vallis-gratiae, Cyrtohypnum versicolor, Ectropothecium regulare, Leucoloma rehmannii, Lopidium pennaeforme, Mittenothamnium pseudoreptans, Oxyrrhynchium subasperum, Pterobryopsis hoenelii* and *Sematophyllum subpinnatum*.

The 47 true Afromontane endemics (mosses that only occur in the southern African section of the Afromontane Region) are listed in Appendix 4 of the Supplementary Information. Species which are largely confined to, and widespread in the Afromontane Region include *Aerobryopsis capensis, Atrichum androgynum, Brachymenium pulchrum, Campylopus stenopelma, Ditrichum brachypodum, Entodon macropodus, Haplocladium angustifolium, Leucobryum acutifolium, Neckera valentiniana, Porotrichum madagassum, Racopilum capense, Rhodobryum umbraculum, Sematophyllum sphaeropyxis* and *Squamidium brasiliense* (see list in Van Rooy, 2000).

Three of the four bryofloristic elements (Cape, Afromontane Grassland, Afromontane Forest) have their main centres of distribution in the Afromontane Region (Van Rooy, 2000). The fourth element (Eastern Highlands) is also well represented in this region by secondary centres.

Drakensberg Domain (3/3)

Area. This domain represents the northern and largest division of the Afromontane Region (Figs 6 & 7). In the TWINSPAN 3+ classification the Drakensberg Domain extends as far south as the forests around George in the Western Cape while the TWINSPAN 5+ classification draws the boundary with the Cape Domain between Port Elizabeth and Grahamstown in the Eastern Cape.

Literature references for the Afromontane Region also apply to this domain. The seed plant flora of the Drakensberg Domain is described in Denys (1980).

Composition of the moss flora. The 409 species/infraspecific taxa that occur in the Drakensberg Domain belong to 179 genera and 50 families (Appendix 1 in Supplementary Information). As with the Afromontane Region, the families Pottiaceae (53 species/infraspecific taxa in 21 genera), Dicranaceae (40 species\infraspecific taxa in 13 genera) and Bryaceae (36 species in eight genera) are the largest in the moss flora of the Drakensberg Domain.

The following eight families (16% of families in this domain) are diagnostic for the Drakensberg Domain: Seligeriaceae (Dicranales), Splachnaceae (Funariales), Eustichiaceae (Bryales), Rhachitheciaceae and Rhabdoweisiaceae (Orthotricales), Prionodontaceae and Trachypodaceae (Isobryales) and Rigodiaceae (Thuidiales).

The genera *Fissidens* (Fissidentaceae) with 24 species, *Bryum* (Bryaceae) with 18 species and *Campylopus* (Dicranaceae) with 17 species are the largest in this Domain. The following 45 genera (25% of genera in this domain) are diagnostic for the Drakensberg Domain: *Abietinella, Aongstroemiopsis, Astomiopsis, Blindia, Callicostella, Campyliadelphus, Chrysohypnum, Conostomum, Cratoneuron,*

Entodontopsis, Eustichia, Herpetineuron, Hyophila, Jaegerina, Lepidopilidium, Leptoischyrodon, Leptoterigynandrum, Leskeella, Levierella, Micropoma, Orthostichopsis, Physcomitrellopsis, Pinnatella, Plagiobryum, Plagiopus, Platyhypnidium, Prionodon, Pterobryopsis, Quathlamba, Rauiella, Rhabdoweisia, Rhachithecium, Rhacopilopsis, Rigodium, Saelania, Sanionia, Stoneobryum, Streptocalypta, Tayloria, Trachypodopsis, Trachypus, Trichosteleum, Tristichium, Vittia and *Weisiopsis*.

The genus *Physcomitrellopsis* (Funariaceae), endemic to the Afromontane Region, is also endemic to the Drakensberg Domain. There are 153 diagnostic species/infraspecific taxa which represent 37% of mosses in this domain (Appendix 5 in Supplementary Information). Of these, 28 species (7%) are endemic to the Drakensberg Domain (Appendix 6 in Supplementary Information). *Quathlamba debilicostata* (Bartramiaceae), listed here as endemic to the Drakensberg Domain, may actually be endemic to the Drakensberg Alpine Domain of the Highlands Region (see below).

Cape Domain (3/4)

Area. The Cape Domain occupies the mountains of the southern and southwestern Cape (Figs 6 & 7). The seed plant phytochorion (Cape Region) covers an area of ± 71,000 km² (White, 1983) or 90,000 km² (Bond & Goldblatt, 1984; Rebelo, 1994; Cowling & Hilton-Taylor, 1997), depending on what figure you accept.

The TWINSPAN 5+ domain (Fig. 7) consists of four distinct areas along the east-west axis of the Cape Fold Belt mountains. In the east, around Alicedale and Grahamstown (grids 3326 A & B), where the Cape Supergroup disappears beneath the

Karoo sediments (Hammerbeck & Allcock, 1985), the Cape mosses form an 'island', separated from the rest of the Cape Domain by an intrusion of the Karoo-Namib Region along the dry Sundays and Great Fish River valleys. The Langeberg (grids 3320 D and 3321 C) represents another Cape island in a sea of Karoo-Namib mosses along the intermontane, low rainfall valleys of the Klein Karoo as well as the coastal plain. The TWINSPAN 3+ domain is also present along the north-south axis of the Cape Fold Belt mountains, as far north as the Cederberge (Fig. 6).

White (1983), Goldblatt & Manning (2000), Van Wyk & Smith (2001) and Rebelo *et al*. (2006) provide information on several aspects of the seed plant (Cape) phytochorion as well as the Fynbos Biome.

Composition of the moss flora. The moss flora of the Cape Domain consists of 284 species/infraspecific taxa in 127 genera and 44 families (see Appendix 1 in Supplementary Information). This represents 59% of species/infraspecific taxa in the Afromontane Region and 57% of all mosses in southern Africa. Pottiaceae (33 species/infraspecific taxa in 17 genera), Dicranaceae (29/11) and Bryaceae (23/7) are the most species-rich among the families in this domain while *Fissidens* of the family Fissidentaceae with 14 species/infraspecific taxa, *Bryum* (Bryaceae) and *Campylopus* (Dicranaceae) with 13 species each, and *Fabronia* (Fabroniaceae) and *Funaria* (Funariaceae) with eight species each are the largest genera.

The Fontinalaceae (Isobryales), probably introduced from Europe (Magill & Van Rooy, 1998), is the only diagnostic family for this domain. The monotypic family Wardiaceae, usually associated with the 'Cape' region, is here shared with the Western Cape Domain of the Karoo-Namib Region as a result of the coarse grain. The genera *Cheilothela*, *Distichophyllum*, *Fontinalis*, *Meiothecium*, *Polytrichastrum* and *Ulota*

are restricted to the Cape Domain but none is endemic to this bryofloristic area. Of the 35 diagnostic species/infraspecific taxa listed in Appendix 7 of the Supplementary Information, the following are endemic to this domain: *Archidium andersonianum, Archidium subulatum, Brachythecium pinnatum, B. pseudopopuleum, B. pseudovelutinum, Breutelia elliptica, B. tabularis, Distichophyllum mniifolium* var. *taylorii, Ephemerum diversifolium, Fabronia wageri, Isopterygium taylorii, Leucobryum rehmannii, Macrocoma pulchella, Macromitrium macropelma, Meiothecium fuscescens, Philonotis comosa, Ulota ecklonii, Weissia cucullata* and *Zygodon leptobolax*.

Karoo-Namib Region (2/3)

Area. This is the second largest bryofloristic region in southern Africa, more or less congruent with the Karoo-Namib regional centre of endemism of White (1983), which extends over an area of 661,000 km². The bryogeographical region is more or less contiguous in the arid to semi-arid, winter rainfall, southwestern corner of the study area, from Port Elizabeth in the Eastern Cape to Lüderitz in southern Namibia (Figs 4 & 5). Both the TWINSPAN 3+ and 5+ classifications show three northern outliers in central Namibia as well as the eastern part of the Northern Cape. In the south the Karoo-Namib Region borders on three Afromontane 'islands' on the mountains of the Cape Fold Belt and follows the dry intermontane valleys down to the coastal plain between Gansbaai in the west and Mossel Bay in the east.

The more or less congruent seed plant phytochorion (Karoo-Namib or Succulent Karoo Region) is described in detail by Goldblatt (1978), Werger (1978a),

White (1983), Takhtajan (1986), Hilton-Taylor (1987, 1994), Jürgens (1991), Cowling *et al*. (1998, 1999) and Van Wyk & Smith (2001).

Composition of the moss flora. The moss flora of the Karoo-Namib Region is composed of 196 species/infraspecific taxa (39% of the total moss flora) representing 93 genera and 37 families (see Appendix 1 in Supplementary Information). Largest among the Karoo-Namib families is the Pottiaceae with 38 species/infraspecific taxa in 19 genera, the Dicranaceae with 19 species/infraspecific taxa in 10 genera and the Bryaceae with 16 species in five genera. The genus *Fissidens* (Fissidentaceae) with 11 species is the best represented in this region followed by *Bryum* (Bryaceae) with 10 species and *Campylopus* (Dicranaceae) and *Funaria* (Funariaceae) with seven species each.

The genera *Acaulon, Crossidium, Cygnicollum*, *Leucoperichaetium, Microcrossidium* and *Pottia* are diagnostic for the Karoo-Namib Region. All but two (*Leucoperichaetium* and *Cygnicollum*) belong to the Pottiaceae. At the time of the numerical analysis *Cygnicollum* of the family Funariaceae and *Microcrossidium* of the Pottiaceae (2% of genera in this region) were endemic to this region. However, moss endemism is expected to increase as a result of the recent discovery of three new moss genera restricted to this area (Hedderson & Zander, 2007, 2008a, 2008b).

Of the 14 diagnostic species (*Acaulon leucochaete, Acaulon recurvatum, Andreaea bistratosa, Archidium amplexicaule, Bruchia queenslandica, Crossidium spiralifolium, Cygnicollum immersum, Fabronia breutelii, Leucoperichaetium eremophilum, Microcrossidium apiculatum, Oligotrichum tetragonum, Pleuridium papillosum* and *Pottia namaquensis)* only *Acaulon leucochaete* (also known from Australia), *Archidium amplexicaule* (South America) and *Bruchia queenslandica*

(Mexico and Australia) are not true endemics. Other important species which are mainly distributed in this region include: *Aloina bifrons, Bryobartramia novae-valesiae, Desmatodon longipedunculatus, Ephemerum namaquense, Funaria clavata, Hennediella longipedunculata, Ischyrodon lepturus, Orthotrichum incurvomarginatum, Phascum peraristatum, Ptychomitriopsis aloinoides, Ptychomitrium crassinervium, Syntrichia chisosa, Tetrapterum tetragonum,* and *Tortula splachnoides.*

Characteristic of the Karoo-Namib moss flora is the prominence of xerophytic mosses, especially the ephemerals, in the families Archidiaceae, Bryaceae, Dicranaceae, Ditrichaceae, Ephemeraceae, Funariaceae, Grimmiaceae and Pottiaceae, adapted to survive life in the semi-arid to arid conditions of this region. Van Rooy (2000) discusses the main life strategies involved and listed the Karoo-Namib mosses belonging to each. Mosses with a Xeropottioid life syndrome are particularly well represented in the Karoo-Namib Region and many taxa in this group occur in Mediterranean and temperate to hot, semi-arid to arid areas of the world, a distribution pattern described as the Xerothermic Pangaean genoelement (Van Rooy, 2000 and references therein).

The moss flora of the Karoo-Namib Region consists mostly of xerophytic species of the Cape Element, and to a lesser degree the Eastern Highlands Element (Van Rooy, 2000). None of the bryogeographical elements has its centre of distribution in this region and the Afromontane Forest Element is poorly represented.

Western Cape Domain (3/5)

Area. The largest of the two Karoo-Namib divisions, the Western Cape Domain covers an area of 54 grid squares, only seven northern grids less than the Karoo-Namib Region. (Fig. 7). It is more or less restricted to the winter rainfall region in the southwestern corner of southern Africa and is known as a centre of unparalleled succulent plant diversity (Hilton-Taylor, 1994; Cowling *et al.*, 1998).

For detailed descriptions of the more or less congruent seed plant (Succulent Karoo) phytochorion, see Werger (1978a), Jürgens (1991), Hilton-Taylor (1987, 1994, 1996), Hilton-Taylor & Le Roux (1989), Milton *et al.* (1997), Cowling *et al*. (1998, 1999) and Van Wyk & Smith (2001).

Composition of the moss flora. The moss flora of the Western Cape Domain is almost identical to that of the Karoo-Namib Region as a whole and only six species (*Fissidens subobtusatus, Barbula bolleana, Funaria rhomboidea, Bryum capillare, B. cellulare* and *Ptychomitriopsis aloinoides*) are not shared between the two phytochoria. The 190 species/infraspecific taxa in this domain represent 93 genera and 37 families (Appendix 1 in Supplementary Information). The moss flora of this domain is characterised by the presence of a substantial number of ephemerals. As in the case of the Karoo-Namib Region, the families Pottiaceae (37 species/infraspecific taxa in 19 genera), Dicranaceae (19 species in 10 genera) and Bryaceae (14 species in five genera) are the largest families while *Fissidens* (Fissidentaceae) with 10 species, *Bryum* (Bryaceae) with eight species and *Campylopus* (Dicranaceae) with seven species are the largest among the genera.

Namaqua Domain (3/6)

Area. The Namaqua Domain is scattered over seven TWINSPAN 5+ grid squares, situated in the most arid part of southern Africa (Fig. 7), generally receiving less than 300 mm of rain per annum. As a result of the many empty grids in this area it is not possible to draw exact boundaries for this domain.

The seed plant flora, vegetation and phytogeography of the Namaqua Domain have been described by Werger (1978a) and Jürgens (1991).

Composition of the moss flora. The Namaqua Domain has the smallest moss flora of all the domains with only 20 species in 15 genera and 10 families (Appendix 1 in Supplementary Information), none of which is diagnostic or endemic to the region.

The presence of xerophytic taxa and the absence of pleurocarpous taxa is striking. The families Pottiaceae (six species in five genera), Bryaceae (four species in two genera) and Funariaceae (three species of *Funaria*) are the best represented in the region. The largest moss genera in the Namaqua Domain are *Bryum* (Bryaceae) and *Funaria* (Funariaceae) with three species each and *Pseudocrossidium* (Pottiaceae) with two species.

Highlands Region (2/4)

Area. The Highlands Region seems to cover the high altitude areas of the Interior Plateau (Figs 4 & 5). Most of the 39 TWINSPAN 5+ grid squares are contiguous along the eastern border with the Afromontane Region, from the northeastern Free State, through Lesotho and the southern Free State, down to the Sneeuberge in the

Eastern Cape. Outliers are present on the Nuweveld mountain range between Beaufort West and Fraserburg in the Great Karoo, the Hantamsberg in the Northern Cape, and the Naukluft Mountains in central Namibia. Another isolated and rather low altitude grid square (2822 C) is found in the Northern Cape and represents a single collecting locality on the southernmost tip of the Langberg.

The region has a temperate climate with summer rainfall, hot summers and cold winters with severe frost and occasional snowfalls. The seed plant vegetation can be classified into alpine and subalpine belts (Killick, 1963, 1978). Although the exact position of the boundary between the Highlands and Afromontane, and Highlands and Karoo-Namib Regions is obscured by the coarse grain of the study as well as empty grid squares, it seems to follow the Great Escarpment for most of the way.

Characteristics of this bryofloristic region are similar to those of the Kalahari-Highveld transition zone of White (1983), including the Drakensberg (Afro-alpine) Region of Killick (1978, 1994), as summarised by Goldblatt (1978), Beentje *et al.* (1994) and Cowling & Hilton-Taylor (1997).

Composition of the moss flora. The moss flora of the Highlands Region is made up of 152 species/infraspecific taxa (30% of the total moss flora) in 71 genera and 29 families (see Appendix 1 in Supplementary Information). The families Pottiaceae (37 species/infraspecific taxa in 16 genera), Bryaceae (21 species in five genera) and Dicranaceae (11 species in five genera) are the largest in this region. The largest genera are *Bryum* (Bryaceae) with 15 species, *Fissidens* (Fissidentaceae) with nine species and *Syntrichia* (Pottiaceae) with eight species/infraspecific taxa.

The Higlands moss flora differs from the closely related Karoo-Namib moss flora mainly in the absence of families such as Bryobartramiaceae, Sphagnaceae and

Wardiaceae as well as ephemerals such as *Acaulon, Bruchia, Crossidium, Cygnicollum, Leucoperichaetium, Microcrossidium* and *Pottia,* and the presence of families such as the Amblystegiaceae, Mniaceae, Thuidiaceae, and additional taxa in the Leskeaceae. The moss flora reflects the severity of the climate and most of the mosses exhibit xeromorphic characters.

There are no diagnostic or endemic families or genera in this region. Two of the three diagnostic species/infraspecific taxa, *Syntrichia austro-africana* (Pottiaceae) and *Physcomitrium spathulatum* var. *sessile* (Funariaceae), are endemic to the Highlands Region while the other, *Pterygoneurum macleanum* (Pottiaceae), is also known from southern and western Australia.

There may actually be more diagnostic and endemic taxa in this region than identified by TWINSPAN but, as a result of the coarse grain, these taxa now fall in predominantly Afromontane grids covering both sides of the KwaZulu-Natal/Lesotho escarpment or the Highlands/Afromontane boundary. Examples are: *Quathlamba debilicostata* (Bartramiaceae), endemic to the escarpment cliffs at Sani Pass, but falls in the Afromontane grid 2929 C, and *Anomobryum drakensbergense* (Bryaceae), endemic to Highlands (2927 B, 2928 B, 3028A) as well as borderline Afromontane grids (2929 A, 2929 C).

Other important species, mainly distributed in this region are: *Bryoerythrophyllum recurvirostrum, Bryum turbinatum, Didymodon trivialis, Encalypta ciliata, Encalypta vulgaris, Ptychomitrium cucullatifolium, P. diexaratum* and *Weissia dieterlenii*.

The Eastern Highlands Element dominates the moss flora of this region (Van Rooy, 2000).

Drakensberg Alpine Domain (3/7)

Area. The Drakensberg Alpine Domain consists of 20 high altitude grid squares contiguous on and around the high plateau of Lesotho (Fig. 7). A group of three outliers occurs in the Sneeuberge between Graaff-Reinet and Middelburg in the Eastern Cape and a single outlier is present in the Hantamsberg north of Calvinia in the Northern Cape. The TWINSPAN 3+ classification shows another outlier (grid 3322 B) in the Swartberg north of De Rust in the Western Cape (Fig. 6).

The climate is severe (broadly classified as temperate with summer rainfall) and the temperature is cool to hot in summer and cold to freezing with snowfalls in winter. The vegetation of the high plateau of Lesotho (mostly above 2750 m) lies in the Alpine belt (Killick, 1963) and has been described as tundra (Killick 1997). Geologically this domain is associated with basalt of the Drakensberg Formation.

Characteristics of the congruent seed plant region is described in detail by Killick (1963, 1978, 1990, 1994, 1997), Schmitz (1984) and Carbutt & Edwards (2004, 2006).

Composition of the moss flora. The moss flora of the Drakensberg Alpine Domain consists of 142 species/infraspecific taxa in 67 genera and 27 families (Appendix 1 in Supplementary Information), only 10 species/infraspecific taxa, four genera and two families less than the Highlands Region. The family Pottiaceae is the largest with 36 species/infraspecific taxa in 16 genera followed by Bryaceae with 20 species in five genera and Dicranaceae with 11 species in five genera. *Bryum* (Bryaceae) with 14 species, *Fissidens* (Fissidentaceae) with eight, and *Syntrichia* (Pottiaceae) and *Funaria*

(Funariaceae) with seven species each are the largest genera in the Drakensberg Alpine Domain.

Syntrichia austro-africana and *Pterygoneurum macleanum*, both of the family Pottiaceae, are diagnostic for the Drakensberg Alpine Domain with *Syntrichia austro-africana* the only endemic taxon. Important Highland species (see list there) are also largely restricted to this domain.

Upper Karoo Domain (3/8)

Area. The Upper Karoo Domain represents the western division of the Highlands Region, scattered over 20 grid squares in the Free State, southern Lesotho, Eastern and Northern Cape as well as Namibia (Fig. 7). This domain occupies a lower altitude and lower rainfall area than the Drakensberg Alpine Domain.

Composition of the moss flora. The moss flora of the Upper Karoo Domain is relatively small and consists of 63 species/infraspecific taxa in 32 genera and 15 families (see Appendix 1 in Supplementary Information). The families Pottiaceae with 18 species/infraspecific taxa in 11 genera, Bryaceae with 12 species in two genera and Funariaceae with eight species/infraspecific taxa in three genera are the best represented in this domain. The largest genera are *Bryum* (Bryaceae) with 11 species, *Funaria* (Funariaceae) with six species and *Fissidens* (Fissidentaceae) with five species.

The Upper Karoo Domain lacks diagnostic, endemic and near-endemic mosses. *Pseudocrossidium crinitum*, *Tortula atrovirens* and *Trichostomum brachydontium* of the Pottiaceae, and *Bryum argenteum* and *B. pycnophyllum* of the Bryaceae are the

most widespread and frequently collected taxa in this domain. *Ptychomitrium cucullatifolium* (Ptychomitriaceae) is widespread and largely restricted to this domain as well as the closely related Drakensberg Alpine Domain.

Of the relatively few pleurocarpous mosses known from the Highlands Region, only six species (four in Leskeaceae, one in Fabroniaceae and one in Meteoriaceae) remain in this domain (see Appendix 1 in Supplementary Information). The pleurocarpous Orders Hookeriales and Hypnobryales, as well as the Sphagnales, Andreaeales and Polytrichales have not been recorded from this domain.

DISCUSSION

Most of the bryofloristic regions identified by the TWINSPAN classifications are fairly geographically homogeneous with adjacent grids being grouped together (Figs 2–7). This suggests that there are clear geographically coherent patterns in the data. There is increased homogeneity of the regions, from the TWINSPAN Complete to the TWINSPAN 5+ classification (Van Rooy, 2000), which has resulted in better definition of some regions, e.g. the Drakensberg Alpine Domain (Highlands Region), but oversimplification of others, e.g. the Cape Domain (Afromontane Region) which has lost its important northwest extension.

Unfortunately the removal of outliers from the TWINSPAN Complete data set resulted in the deletion of most grid squares in the already undercollected, arid northwestern sector of the study area or the countries of Namibia and Botswana and large parts of the Northern Cape, Free State and North-West. This has made it impossible to present a clear picture of bryogeographical regions in this area, corroborating the conclusions of others (e.g. Linder, 1998) who, in a numerical

analysis of African plant distribution patterns, found that the arid areas of Namibia and Botswana are “as yet too poorly sampled to give a robust indication of their phytochorological affinities".

The first and major TWINSPAN division line is not clearly distinguishable, especially in the central and northern parts of the study area, mainly due to the many empty grid squares, but also as a result of the grain chosen for this study (Figs 2 & 3). This is to be expected in an exploratory, broad-scale analysis where the general pattern of division is more important than the precise boundaries between groups. However, the main discontinuity in the data appears to coincide with sections of major geological, physiographical, climatic, ecological and phytogeographical division lines in southern Africa (van Rooy, 2000). Whether this line represents the boundary between two bryofloristic kingdoms, or the boundary between phytochoria of a lower rank, is not clear at this stage and should be determined by a much broader study including the whole of Africa and other southern temperate areas. We therefore refrain from assigning a formal rank to the two main bryofloristic regions of southern Africa.

The main subtropical or palaeotropical region (1/1) occupies the northern, eastern and southern parts of southern Africa while the temperate or austral region (1/2) covers the central and western parts (Figs 2 & 3). The moss flora of the subtropical region is predominantly mesophytic while the temperate region is characterised by a xerophytic moss flora, including the ephemerals (see Appendix 1 in Supplementary Information). Pleurocarpous mosses make up an increasingly larger proportion of the moss flora as one moves from temperate areas in the western and central part of southern Africa, to subtropical areas in the east, north and south.

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SUPPLEMENTARY INFORMATION

Supplementary information may be found in the online version of this article:

Figure 1. Dendrogram of the TWINSPAN 3+ classification of ½° grid squares.

Figure 2. Dendrogram of the TWINSPAN 5+ classification of ½° grid squares.

Appendix 1. The moss floras of the bryofloristic regions

Appendix 2. Diagnostic genera of the Afromontane Region

Appendix 3. Diagnostic species of the Afromontane Region

Appendix 4. Afromontane endemics

Appendix 5. Diagnostic species of the Drakensberg Domain

Appendix 6. Drakensberg Domain endemics

Appendix 7. Diagnostic species of the Cape Domain

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FIGURE CAPTIONS

Figure 1. The distribution of altitudes over the Flora of Southern Africa (study) area.

Figure 2. The two main bryofloristic regions of southern Africa as delimited by the TWINSPAN 3+ classification of ½° grid squares.

Figure 3. The two main bryofloristic regions of southern Africa as delimited by the TWINSPAN 5+ classification of ½° grid squares.

Figure 4. The bryofloristic regions of southern Africa as delimited by the TWINSPAN 3+ classification of ½° grid squares.

Figure 5. The bryofloristic regions of southern Africa as delimited by the TWINSPAN 5+ classification of ½° grid squares.

Figure 6. The bryofloristic domains of southern Africa as delimited by the TWINSPAN 3+ classification of ½° grid squares.

Figure 7. The bryofloristic domains of southern Africa as delimited by the TWINSPAN 5+ classification of ½° grid squares.

FIGURES

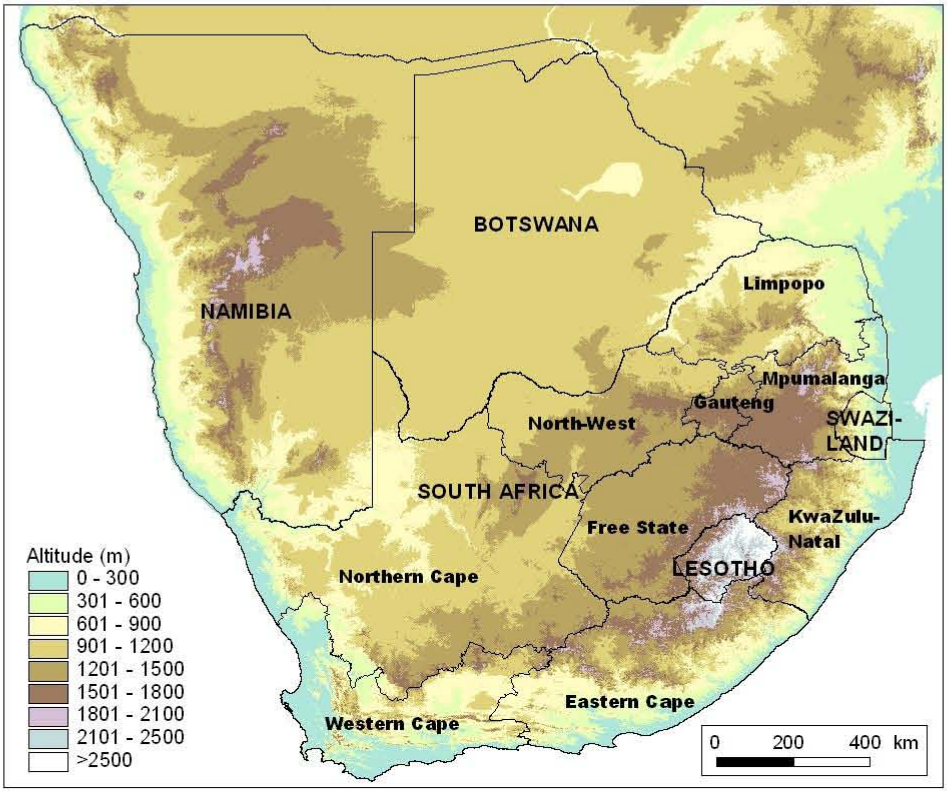
BOTSWANA
NAMIBIA
Limpopo
Mpumalanga
Gauteng
North-West
SWAZI-
LAND
SOUTH AFRICA
Free State
KwaZulu-
Natal
LESOTHO
Northern Cape
Eastern Cape
Western Cape
Altitude (m)
0 - 300
301 - 600
601 - 900
901 - 1200
1201 - 1500
1501 - 1800
1801 - 2100
2101 - 2500
>2500
0 200 400 km

Figure 1

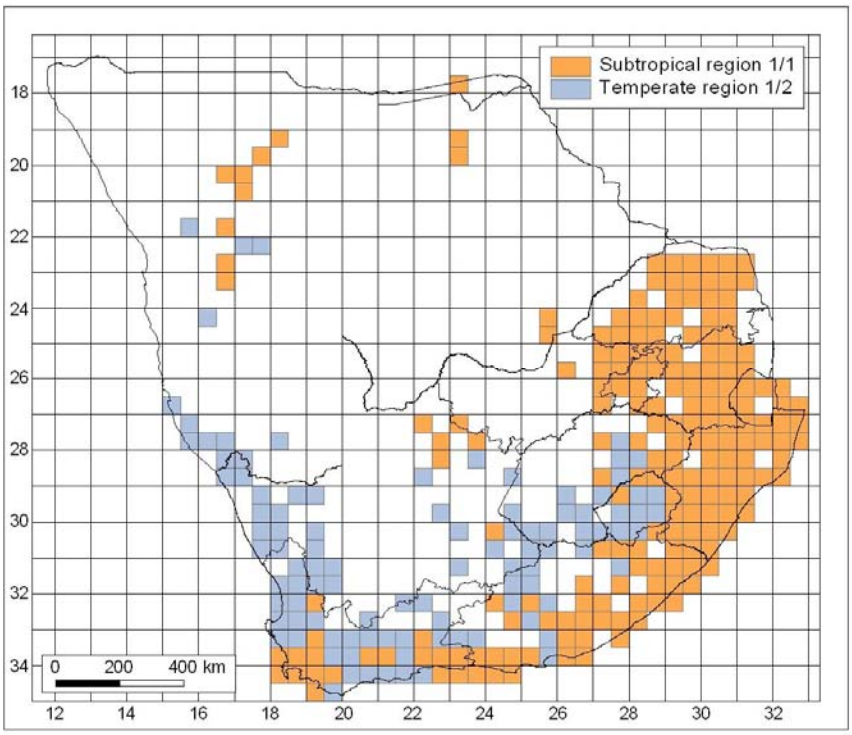

Figure 2

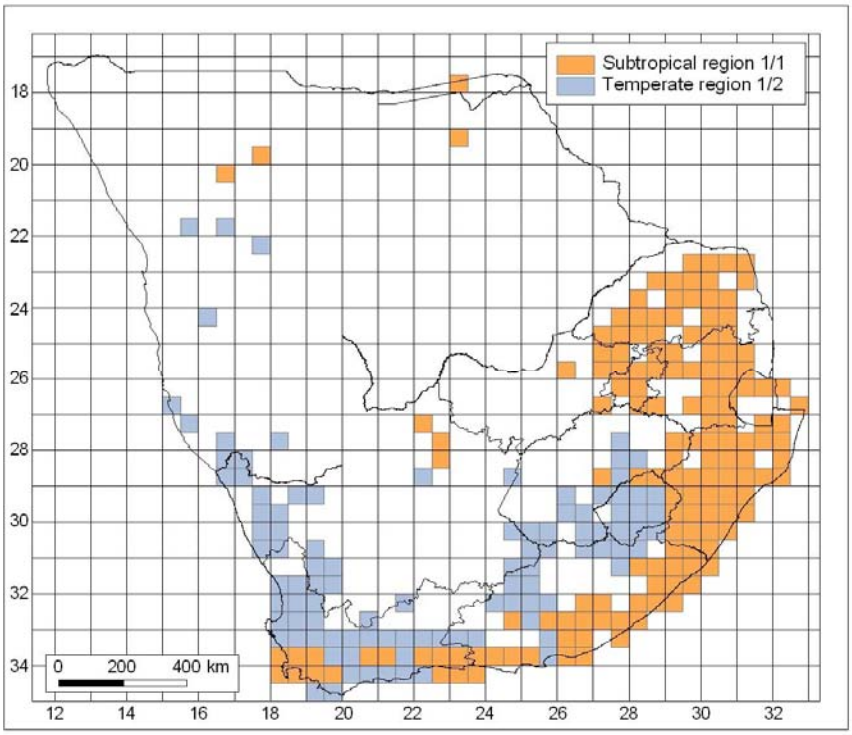

Figure 3

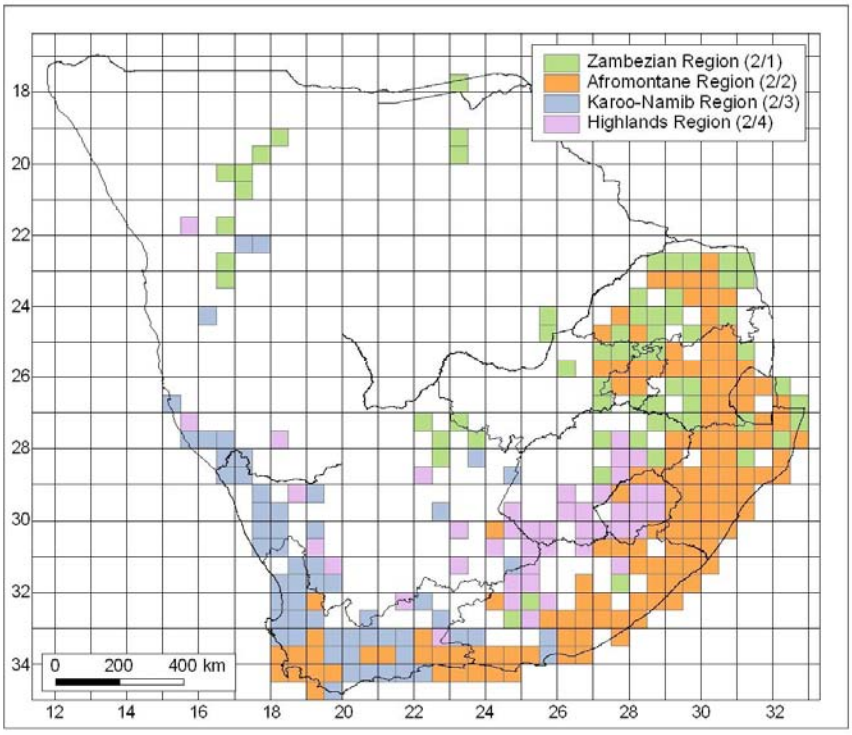

Figure 4

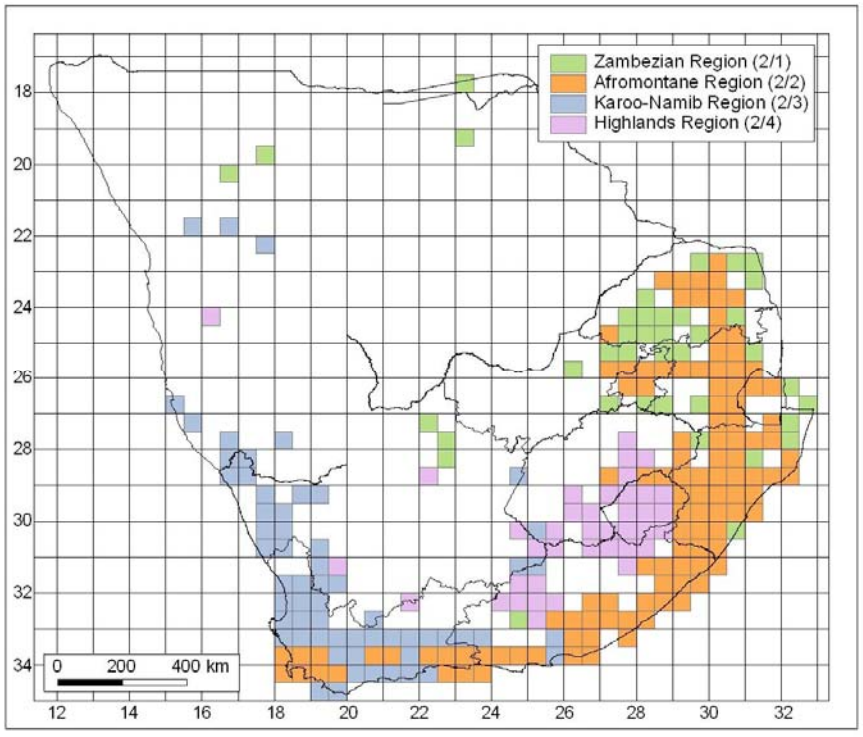

Figure 5

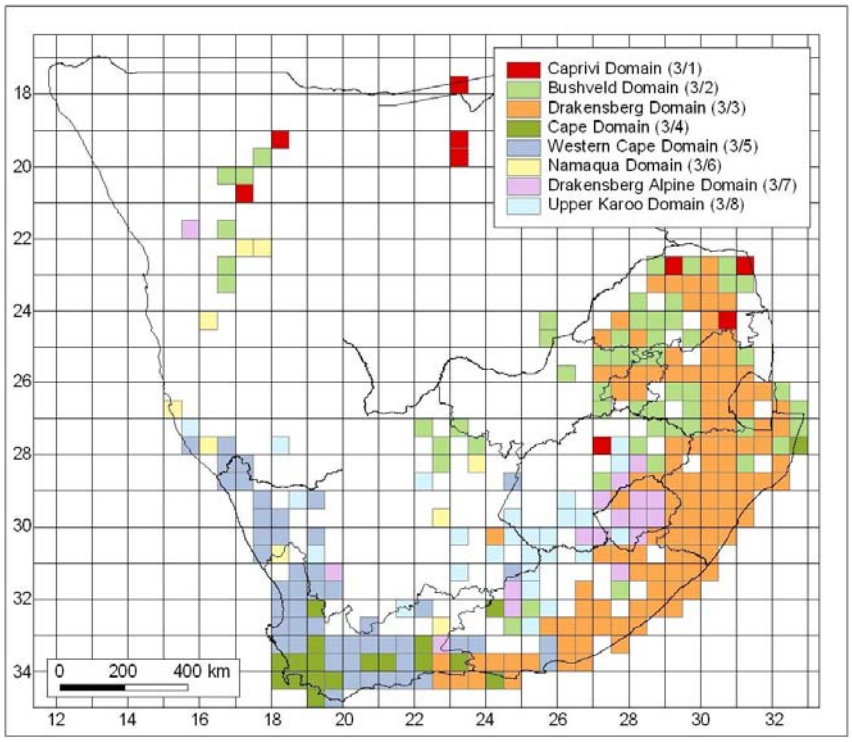

Figure 6

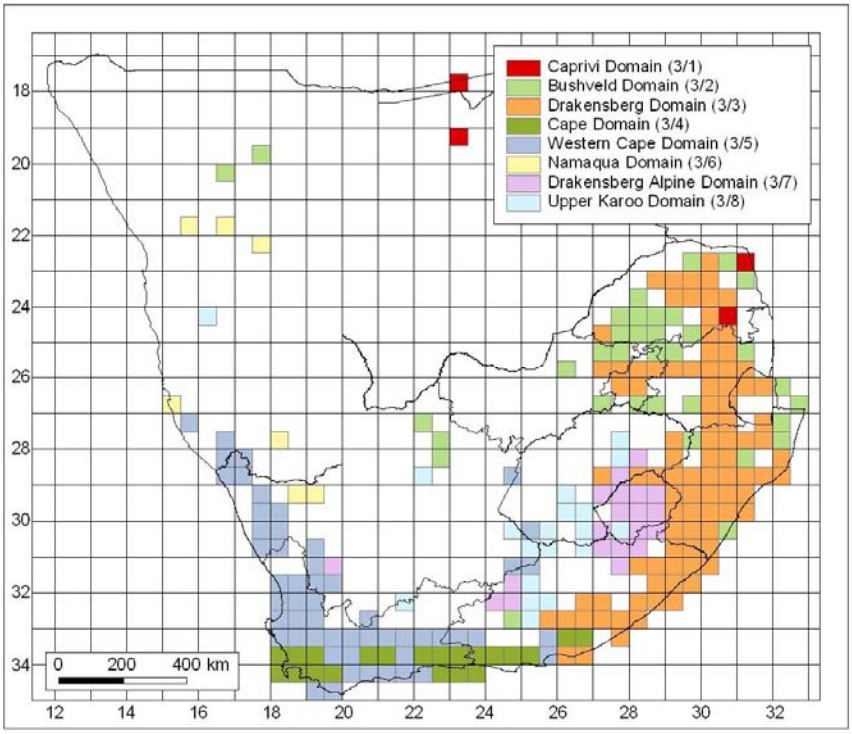

Figure 7