

Floristic endemism in southern Africa: A numerical classification at generic level

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A hierarchy of phytogeographic regions within southern Africa south of the Kunene, Okavango, and Limpopo Rivers, is suggested. A numerical classification technique, the TWINSPLAN computer program, has been used to analyse the distribution data for seed plant genera endemic to the region, as reflected by the PRECIS database of the National Herbarium, Pretoria. Four main phytochoria have been identified. These are the Kaokoveld region in northern Namibia, the Kalahari region, the Greater Afromontane region in the eastern parts of South Africa, and the large, south-western, Greater Cape region. Both the Greater Afromontane and the Greater Cape region have been subdivided into further groupings representing phytochoria at lower levels of the hierarchy. At least 586 seed plant genera are endemic to southern Africa, the largest of these being *Aspalathus* (Fabaceae) with 278 species. The Mesembryanthemaceae contribute the largest number (114) of endemic genera. Almost half of the genera endemic to southern Africa are monotypic, suggesting the presence of a very old and stable flora in this region. Areas of high diversity in terms of endemic genera have also been mapped.

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Introduction

Background

The diversity and phytogeography of the exceptionally rich vascular plant flora of southern Africa have been the subject of many stud-

ies. Among the publications that had a significant influence on current views of the flora, vegetation and phytogeography of southern Africa are Acocks (1953), Goldblatt (1978), Werger (1978), White (1983), Rutherford and Westfall (1986), Cowling *et al.* (1989), Cowling

and Hilton-Taylor (1994, 1997), Irish (1994), Low and Rebelo (1996), Cowling *et al.* (1997), Jürgens (1997) and Barnard (1998).

Recently, van Wyk and Smith (2001) published a comprehensive treatise on regions and centers of floristic endemism in southern Africa – a publication that prompted the current series of analyses of the distribution patterns of genera endemic to the region. This publication covers the African subcontinent south of the Kunene, Okavango, and Zambezi Rivers (Fig. 1). Although the authors did not attempt a formal hierarchical classification of the areas of endemism in southern Africa, they did identify three larger ‘Regions of Endemism’ which would be of a higher rank than the 18 local ‘Centres of Endemism’ that they recognise (Fig. 1). These three regions are the Cape Floristic Region, a phytochorion that more-or-less coincides with the Cape Floristic Kingdom, the Succulent Karoo Region that includes the Gariep, Knersvlakte, Little Karoo, Worcester-Robertson Karoo, and Hamtam-Roggeveld Centres, and the Maputaland-Pondoland Region that includes the Pondoland and Maputaland Centres of Endemism (Fig. 1). In addition to the 18 centres of endemism that were formally recognised, mention was also made of several other possible centres of endemism such as the Tanqua Karoo, Steytlerville Karoo, Mt. Ngeli, Tugela River Valley, the Wakkerstroom area, the Nkandla Forest area, the Waterberg Mountains of the Limpopo Province, the middle Limpopo River Valley, the Barotse Centre on Kalahari sands and several others. The recognition and demarcation of centres of endemism in van Wyk and Smith (2001) were based mainly on a synthesis of published information, a critical assessment of observed and reported plant distribution information, and the authors’ combined taxonomic and field experience in the region; no numerical techniques were employed. The only significant numerical

study on phytochoria in southern Africa is that by van Rooy (2000) on the moss flora of the region. The present study is a first attempt towards a numerical, hierarchical classification of floristic regions in southern Africa based on binary presence-absence distribution data of the c. 600 seed plant genera endemic to the region.

Some readers may query our use of genera instead of species in this study, as surely, it is reasonable to expect to obtain more meaningful results by using more taxa (as represented by species instead of genera). There are two responses to this argument. Firstly, taxa of higher taxonomic rank have traditionally been used to delimit larger phytogeographical regions. Takhtajan (1986), has for example, used plant families and genera to divide the world up into floristic kingdoms and regions. As we were working at the regional and not local scale in this study, we thought it appropriate to rather use genera instead of species in the analysis. Secondly, we wanted to determine whether the use of genera in a numerical phytogeographical study would result in informative, interpretable biogeographical patterns.

Study Area

The study area (hereafter referred to as southern Africa or the *Flora of Southern Africa (FSA)*-region) occupies the southern tip of Africa south of the Kunene, Okavango and Limpopo Rivers (Fig. 2). It includes the countries of Botswana, Lesotho, Namibia, South Africa and Swaziland (Fig. 2) and covers an area of c. 2.7 million km² (Cowling *et al.* 1997). The nine provinces of South Africa referred to in the text are in the north: Limpopo and North-West; in the east: Mpumalanga, KwaZulu-Natal and Eastern Cape; centrally: Gauteng and the Free State, and in the west: Northern Cape and Western Cape (Fig. 2).

Geomorphologically, southern Africa is characterised by a high interior plateau,

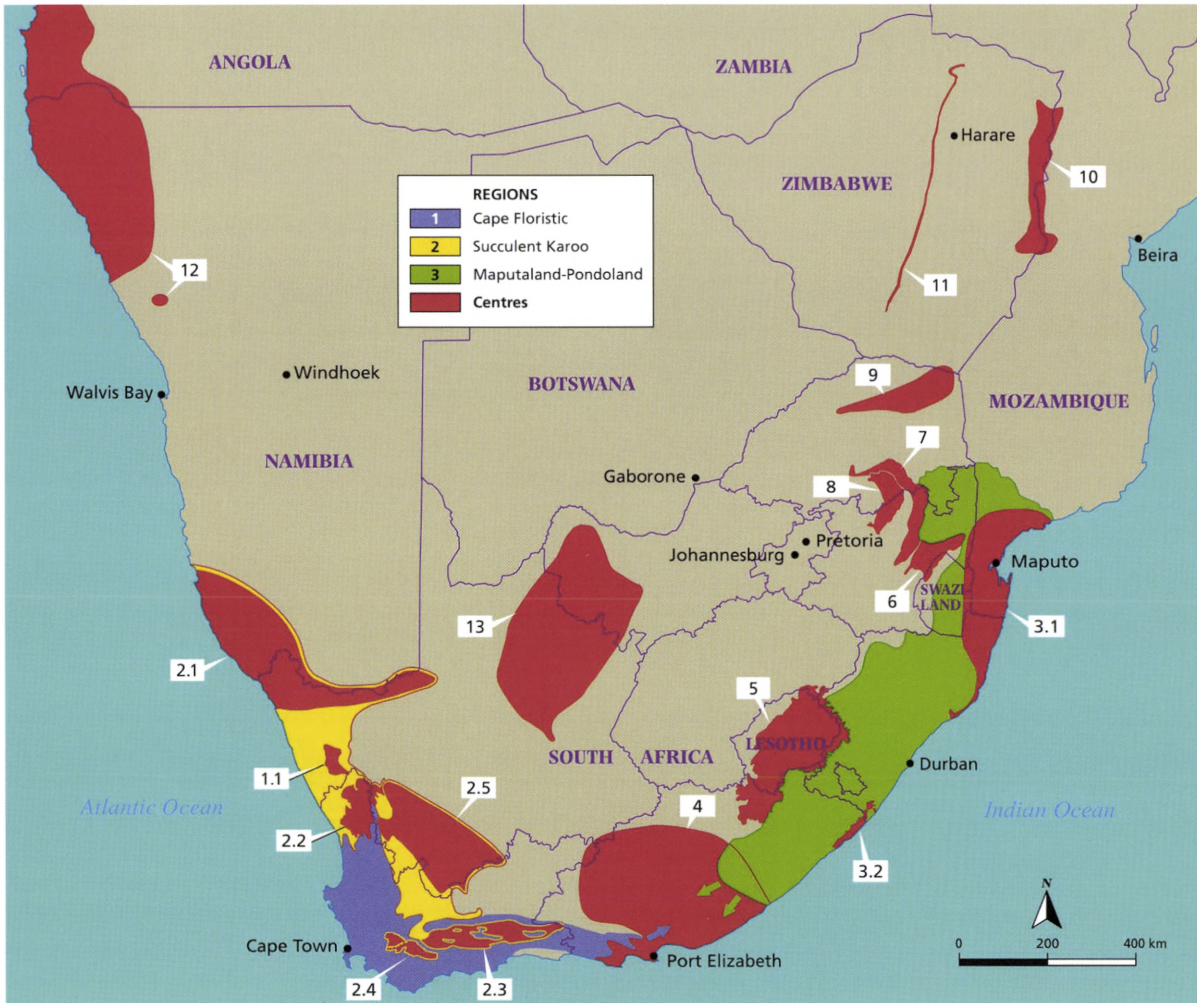


Fig. 1. Principle regions and centres of plant endemism in southern Africa. Note that this map indicates not only the FSA-region, but also the countries bordering it, namely Angola, Zambia, Zimbabwe and Mozambique. Names of the various regions and centres are supplied below. Extensions (arrows) of the Cape Floristic Region and the Maputaland-Pondoland Region into the Albany Centre have not been mapped. From: van Wyk & Smith (2001), *Regions of floristic endemism in southern Africa: a review with emphasis on succulents*.

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|--------------------------------------|-------------------------------|
| 1. Cape Floristic Region | 4. Albany Centre |
| 1.1 Kamiesberg Centre | 5. Drakensberg-Alpine Centre |
| 2. Succulent Karoo Region | 6. Barberton Centre |
| 2.1 Gariiep Centre | 7. Wolkberg Centre |
| 2.2 Knersvlakte Centre | 8. Sekhukhuneland Centre |
| 2.3 Little Karoo Centre | 9. Soutpansberg Centre |
| 2.4 Worcester-Robertson Karoo Centre | 10. Chimanimani-Nyanga Centre |
| 2.5 Hantam-Roggeveld Centre | 11. Great Dyke Centre |
| 3. Maputaland-Pondoland Region | 12. Kaokoveld Centre |
| 3.1 Maputaland Centre | 13. Griqualand West Centre |
| 3.2 Pondoland Centre | |

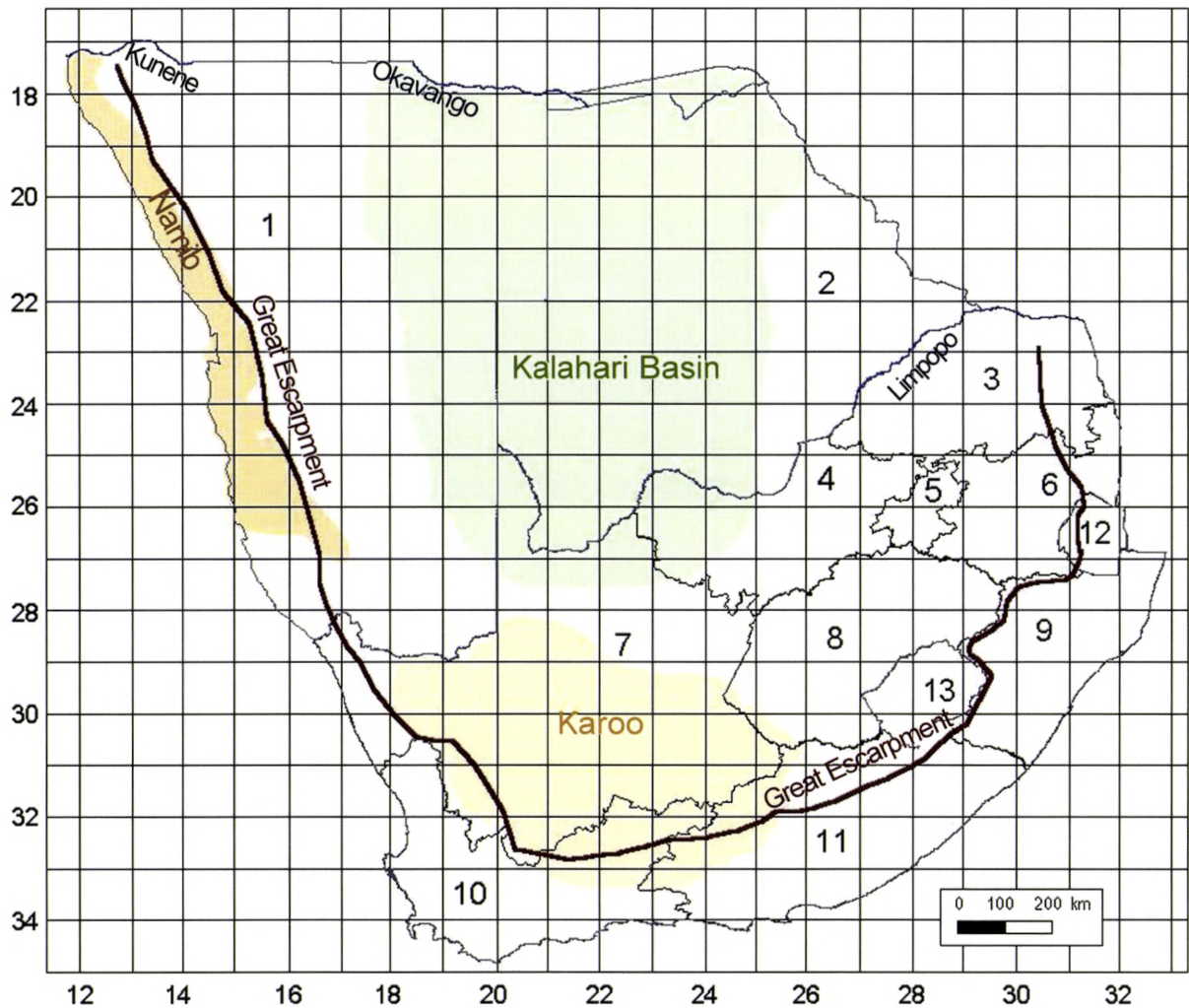


Fig. 2. Map of the study area indicating the following regions and geographical entities referred to in the text: the Kalahari, Karoo, and Namib regions, the Limpopo, Okavango, and Kunene Rivers, and the Great Escarpment. Numbers indicate the following countries and provinces:

- | | |
|---------------------------------------|---------------------------------|
| 1. Namibia | 8. Free State (South Africa) |
| 2. Botswana | 9. KwaZulu-Natal (South Africa) |
| 3. Limpopo Province (South Africa) | 10. Western Cape (South Africa) |
| 4. North-West Province (South Africa) | 11. Eastern Cape (South Africa) |
| 5. Gauteng (South Africa) | 12. Swaziland |
| 6. Mpumalanga (South Africa) | 13. Lesotho. |
| 7. Northern Cape (South Africa) | |

bounded on three sides by the Great Escarpment (Fig. 2). The escarpment comprises a number of distinct mountain ranges, and

reaches its highest altitudes in KwaZulu-Natal and especially in Lesotho. In Namibia the escarpment forms the natural boundary between

the Namib Desert and the interior plateau. The inland plateau characterises large parts of South Africa and Namibia, and all of Botswana. Below the escarpment lies the coastal plain, 50-200 km wide, in places deeply dissected by river gorges (Schulze 1965; Partridge & Maud 1987; Tyson 1987; Moon & Dardis 1988; Reader's Digest 1994; Schulze 1997; Tyson & Preston-Whyte 2000). Most of the floristic diversity of the subcontinent is centered on and around the Great Escarpment, as well as on the coastal plains. The inland plateau is floristically relatively impoverished. Southern Africa, and especially South Africa, also has a very diverse and complex geology that influences plant distribution patterns in the region (Visser 1989; Viljoen & Reimold 1999).

Southern Africa can be classified as semi-arid, with less than 5% of the region receiving an annual rainfall of greater than 800 mm, and on average, more than 90% of rainfall return to the atmosphere through evaporation (Cowling *et al.* 1997). Average runoff constitutes approximately 9% of the total rainfall (Schulze 1997). The average mean rainfall for South Africa and Namibia is c. 500 mm and c. 250 mm respectively (Schulze 1965; Tyson 1987; Reader's Digest 1994; Barnard 1998; Tyson & Preston-Whyte 2000). There is a steep climatic gradient from the hyper-arid and foggy Namib Desert along the west coast, to the hot and humid east coast of South Africa. Most of the study area can be described as a summer-rainfall area, with a winter-rainfall area occurring in the southwest corner, extending along the west coast to southern Namibia, and an all year rainfall area along the southern Cape coast. These climatic patterns are mostly a result of the temperate-tropical convergence zone, with the cold Benguela Current along the west coast and the warm Agulhas Current along the east coast, along with the varied topography described above (van Rooy 2000).

For a temperate, semi-arid region, southern

Africa is exceptionally rich in vascular plants. It is estimated that more than 10% of all vascular plants, including 46% of all succulents, occur on this subcontinent south of the Kunene and Zambezi Rivers, an area covering less than 2.5% of the world's land surface area (van Wyk & Smith 2001). It is further estimated that at least 60% of the flora are strictly confined (endemic) to this region (van Wyk & Smith 2001). These high levels of endemism do not arise only at the species and infraspecific taxonomic ranks, but also extends to genera, of which approximately 20-30% have been estimated to be endemic to southern Africa. The southwestern Cape, Succulent Karoo, Maputaland-Pondoland, and Afromontane regions are especially rich in vascular plants (van Rooy 2000).

Southern Africa is divided into eight biomes based primarily on vegetation structure and certain climatic patterns (Rutherford & Westfall 1989; Low & Rebelo 1996; van Wyk & Smith 2001). Covering the largest part of the study area, including most of the eastern parts of Namibia, almost all of Botswana, and the northernmost parts of South Africa is the Savanna Biome, structurally characterised by a tree and a grass layer. Covering the higher parts of the inland plateau (the Highveld) and the eastern escarpment is the Grassland Biome. The Nama-Karoo Biome, a low shrubland, stretches along the western parts of Namibia, just east of the Namibian western escarpment, and spreads out on the arid, western, lower plateau in South Africa. The Desert Biome is confined to the west coast of Namibia, while the Succulent Karoo, characterised by high numbers of succulent plants, stretches along the extreme southwestern coast of Namibia and west coast of South Africa. The Fynbos Biome, characterised by many taxa with fine, sclerophyllous leaves, occupies the southern most tip of Africa, and stretches along the southeast coast into the Eastern Cape. The Thicket Biome, a dense, almost impenetrable,

tall shrubland occurs particularly in most of the hot and dry river valleys along the east coast. The Forest Biome is characterised by a tall tree layer, epiphytes and lianas, and occurs in patches along the southern, eastern and northern coasts and escarpment of South Africa. In the study area, the geophytic life form is a significant component of the Fynbos, Succulent Karoo, and Grassland biomes.

Definitions of Concepts

It was deemed necessary to provide a short list of key definitions to ensure that our intent, understanding and application of some (sometimes confusing or misapplied) phytogeographical terms used in this paper are clear and unambiguous.

Centre of diversity: An area with a high concentration of taxa within the total geographic distribution of a particular flora or element of a flora.

Centre of endemism: An area with a high concentration of taxa with limited geographic distributions (endemics).

Phytogeographic (floristic) region: A group of grid-areas of similar floristic composition. A phytogeographic region can also be described as a natural area with a characteristic flora (McLaughlin 1994). Phytogeographic or floristic regions can not overlap geographically but may share a number of taxa. Generally, when we use the term 'region' in isolation, in this paper, we refer to a phytogeographic region or phytochorion.

Phytogeographic (floristic) elements: A group of taxa with similar geographical distributions. The distributions of different phytogeographic elements may overlap, but a taxon at a specific taxonomic rank may only belong to one element. (To clarify: a particular species may belong to one phytogeographic (floristic) element, but when considered at the genus level – as part of a larger whole – it may belong to another phytogeographical element).

Phytochorion: A phytochorion is a phytogeographic (floristic) region or area of any rank.

Region of endemism: A natural phytogeographic (floristic) region determined by only the endemic component of the total flora. It is not necessarily distinguished by a high concentration of endemics as in the case of a centre of endemism. (In the present paper we attempt to demarcate regions of endemism based on the geographical distribution of *genera* endemic to the FSA-region.)

We use the terms 'phytochorion' and 'region of endemism' interchangeably in this paper, as a phytochorion is, in essence, a 'region of endemism', just at any rank in the hierarchy. We can say this because endemic taxa have traditionally been one of the major diagnostic characters used to define and delimit phytochoria (see for example Takhtajan 1986 and White 1983).

Aims and Objectives

The main aim of this study was to test whether a numerical analysis (in this case using TWINSpan) of distribution data of plant genera endemic to the southern Africa region, obtained from the mega-database PRECIS, will result in interpretable and informative biogeographical patterns. The second aim was to obtain a hierarchy of phytogeographical regions, but not a formal classification into ranks (for example Kingdom, Subkingdom, Region, Domain, Sector, and District), using the numerical analysis technique and distribution data mentioned above. We have also included some statistics on the genera endemic to southern Africa.

Background on PRECIS

The compilation of the PRECIS database started in the 1970s with the computerisation of herbarium specimens of the National

Herbarium in Pretoria (PRE). Since then it has been extended to include records from the Compton Herbarium in Kirstenbosch (NBG) and the Natal Herbarium in Durban (NH). Since 1996, under the auspices of the Southern African Botanical Diversity Network (SABONET), computerisation of herbarium specimens, using the PRECIS mega-database, has also been started (and in one case completed) in selected herbaria in Angola, Botswana, Lesotho, Malawi, Mozambique, Namibia, Swaziland, Zambia and Zimbabwe. These databases will be, and are in the process of being, incorporated into the main PRECIS server housed at PRE. PRECIS consists of a several components, the two main ones being the specimen and the taxon databases (Prentice & Arnold 1998). These two sub-databases, among them, can house a myriad of information on the nomenclature, biology, ecology, distribution, and economic uses at any level of the taxonomic hierarchy, and information about type status, site of collection, phenology, name of collector and other information usually included on a specimen label at the specimen level (Prentice & Arnold 1998). PRECIS is the single largest digital repository of botanical information in Africa. Currently only approved users have access to PRECIS, but the intention is for it to be available for anyone to use freely.

Material and Methods

Leistner (2000) was consulted to compile a list of seed plant genera endemic to the study area. Distribution records for these genera were obtained from the National Herbarium, Pretoria (PRE) Computerised Information System (PRECIS). A list of about 25 genera added to the PRECIS database after the publication of Leistner (2000) has also been obtained from the database. These genera were either newly described (e.g. *Roodebergia*) or reinstated (e.g. *Lydenburgia*). Though distribution records for

these genera were sparse and incomplete, 13 were judged endemic to southern Africa, and were included in the dataset used in the present study. Another c. 20 genera are possibly endemic to southern Africa, but were not included in the dataset due inadequate information on their distribution ranges. Thirty-four of the genera that were identified as being endemic to southern Africa had no distribution record in PRECIS, even though their distribution ranges are known in the literature, and has therefore been excluded from this first attempt at a numerical classification, but not from the larger dataset used for statistical calculations. We have also added a few genera that we know are near-endemic to the region, for example those that just enter into southern Mozambique and southern Angola, in order to reduce border effects in the classification.

The dataset obtained from Leistner (2000) and PRECIS were compiled into a binary presence-absence data matrix and inputted, via Turboveg 1.97 (International Single User Version, Stephen Hennekens) and Megatab 2.2 (Elsware) into the computer program TWINSpan (two-way indicator species analysis) (Hill 1979) for a numerical classification. TWINSpan is a divisive, hierarchical classification technique that detects overall patterns of differences in biological data (Moreno Saiz *et al.* 1998; Ojeda *et al.* 1998; van Rooy 2000; Lawesson & Skov 2002 and references therein). One of the key premises of TWINSpan is that for each set of sample-grids (in this study quarter-degree grid squares), a dichotomy can be made with one set of sample-grids at the one side, and another on the other side (Kent & Coker 1994). TWINSpan has been chosen for its proven combination of effectiveness, robustness, relative objectivity, availability and speed (Gauch & Whittaker 1981; van Rooy 2000). TWINSpan has also been judged the best general-purpose method, especially when a data set is 'complex, noisy,

large or unfamiliar' (Gauch & Whittaker 1981), as in the case of the dataset used in this study.

Results of both the original TWINSpan classification, and of some subsequent classifications that were carried out on selected subsets of the original classification are presented as a simplified dendrogram and plotted on maps. The dendrogram showing the hierarchy of phytochoria in the study area has been drawn manually after TWINSpan has been run on the dataset. Using the results from the TWINSpan analysis, point files (*.pnt) of the different phytochoria, containing the quarter-degree grids that fall under any given phytochorion, have then been compiled for use in the MAPPIT computer program for compiling the maps. Those sections of the dataset that was deemed very large and homogeneous were then subjected to further TWINSpan analyses. The whole dataset was subjected to only one TWINSpan run, while two larger subsets (called the Greater Afromontane and Greater Cape regions in the results and discussion) underwent two TWINSpan analyses each. A single smaller subset from the Greater Cape subset mentioned above underwent a third TWINSpan analysis. The dendrogram and maps presented were compiled from the hierarchy suggested by the results of the cumulative TWINSpan analyses following a similar procedure as that described above for the first run of the TWINSpan analyses.

The MS-DOS computer program MAPPIT 2.0 (1996) (privately owned software developed by the South African National Biodiversity Institute) was used for the translation of distribution records into a format useable by ArcView 3.1 (1992-1996) (Environmental Systems Research Institute, Inc), while ArcView was used for the production of the maps. MAPPIT has been developed specifically to run in conjunction with PRECIS. A map depicting centres of diversity was produced using

ArcView. Only phytogeographic (floristic) regions, and not phytogeographic (floristic) elements, were identified and arranged into a hierarchy.

The FSA region was selected as study area as PRECIS distribution records are the most complete for this part of the subcontinent. Three sample-grid sizes were contemplated, full-degree grid squares, half-degree grid squares, and quarter-degree grid squares. Half-degree grid squares were considered the most appropriate for a study at this scale. However, as quarter-degree grid squares is the standard format in which distribution data is captured into PRECIS, this smaller sample-grid size was used instead, even though it might result in more 'noise' in the dataset and on the map (van Rooy 2000). Full-degree grid squares were considered inappropriate as boundaries between phytochoria might be obscured when this sample-grid size is used (van Rooy 2000).

Results

The dataset indicate that 586 seed plant genera, belonging to 80 families are endemic to the FSA region. This figure may obviously vary, depending on the particular classification systems adopted for the various groups. Another

Table 1. Ten largest genera endemic to southern Africa, the families they belong to, and their number of species.

Genus	Family	No. of species
<i>Aspalathus</i>	Fabaceae	278
<i>Ruschia</i>	Mesembryanthemaceae	224
<i>Lampranthus</i>	Mesembryanthemaceae	220
<i>Agathosma</i>	Rutaceae	140
<i>Drosanthemum</i>	Mesembryanthemaceae	120
<i>Lachenalia</i>	Hyacinthaceae	110
<i>Antimima</i>	Mesembryanthemaceae	99
<i>Conophytum</i>	Mesembryanthemaceae	88
<i>Geissorhiza</i>	Iridaceae	84
<i>Leucadendron</i>	Proteaceae	83

Table 2. Ten plant families with the largest number of genera endemic to southern Africa, the number of species in these genera, the largest endemic genus in each family and its number of species.

Family	No. of endemic genera	Total no. of species in family belonging to endemic genera	Largest endemic genus in family	No. of species in largest genus
Mesembryanthemaceae	114	1444	<i>Ruschia</i>	224
Asteraceae	96	480	<i>Metalasia</i>	52
Scrophulariaceae	31	235	<i>Diascia</i>	60
Asclepiadaceae	28	108	<i>Quaqua</i>	19
Fabaceae	20	527	<i>Aspalathus</i>	278
Iridaceae	18	278	<i>Geissorhiza</i>	84
Restionaceae	18	239	<i>Ischyrolepis</i>	49
Hyacinthaceae	16	170	<i>Lachenalia</i>	110
Poaceae	16	60	<i>Merxmuellera</i>	17
Apiaceae	16	47	<i>Anginon</i>	12

ca. 20 genera are possibly endemic to the region, but were not included in the dataset due to insufficient and uncertain distribution records. Approximately 3,049 indigenous and 456 naturalised seed plant genera occur in the region. This means that 19.2% of the seed plant genera that naturally occur in southern Africa are endemic to the region. A combined total of 4,907 species are included in these endemic genera. The ten largest endemic genera, with their number of species and the families they belong to are listed in Table 1. The ten seed plant families with the largest number of endemic genera, the number of endemic genera they contain, each family's largest endemic genus and the number of species the largest genus contains are listed in Table 2. The ten endemic genera that were recorded for the highest number of quarter-degree grid squares in PRECIS, and the number of quarter-degree grid squares in which they occur, are listed in Table 3. Note that these genera are not necessarily those with the geographically largest overall distribution ranges. Two hundred and five (34.9%) endemic genera are monotypic. A size distribution divided into 12 intervals is represented in Fig. 3. Note that the last three intervals are much larger than the others due

to the small number of genera that reach these sizes. Fig. 4 is a map depicting regions of high diversity for endemic genera in southern Africa. Fig. 5 shows collecting intensity in southern Africa, at the specimen level, according to PRECIS records.

The results of the TWINSpan classification are presented as a simplified dendrogram in Fig. 6. The higher levels of the classification (phytogeographical regions 1-4) are illustrated as a map in Fig. 7. Lower level phytogeographical regions (subgroups of regions 2 and 3) are

Table 3. The ten genera endemic to southern Africa that occur in the largest number of quarter-degree grids according to PRECIS.

Genera	Number of quarter-degree grids in PRECIS
<i>Heliophila</i>	452
<i>Eriocephalus</i>	437
<i>Haemanthus</i>	388
<i>Melolobium</i>	373
<i>Ruschia</i>	341
<i>Nerine</i>	319
<i>Aspalathus</i>	318
<i>Watsonia</i>	304
<i>Brunsvigia</i>	289
<i>Diascia</i>	274

illustrated as a map in Fig. 8. The TWINSpan classification resulted in the identification of four main phytogeographical regions (Figs 6, 7). First to split off from the rest was the Kaokoveld phytochorion (main group 4) in northern Namibia – a region that closely approaches the Kaokoveld Centre of Endemism (Fig. 1) of van Wyk & Smith (2001). The second main phytogeographical region to split off from the main body was the Kalahari region (main group 1) (Figs 6, 7). The largest part of the region is then divided into the Greater Afromontane (main group 2) and Greater Cape (main group 3) regions. At the lower levels of the hierarchy (Figs 6, 8), the Greater Mputaland region (2.1), stretching from northern KwaZulu-Natal around the northern higher mountains to the Highveld region, is the first region to split off from the rest of the Greater Afromontane phytochorion (2). The second region to split off is the Drakensberg Alpine region (2.2.1), leaving only the Highveld region (2.2.2.2) and the Core Afromontane region (2.2.2.1). The arid Northwestern Karoo phytochorion (3.2) is the first to split off from the Greater Cape region (3); followed by the Central Karoo (3.1.2.2) and Northern Succulent Karoo (3.1.2.1) regions. Next is the

Southern Succulent Karoo (3.1.1.2), followed by the Northwestern (3.1.1.2) and Southeastern (3.1.1.1.1) Fynbos regions.

Discussion

The intention in this study was mainly to observe patterns of phytochorion distribution in southern Africa as identified by a numerical classification, thereby judging the efficiency of such a technique, and not to identify the processes responsible for these observed patterns. A *formal* interpretation of the observed patterns is therefore not included in this discussion. (See the discussions of the study area under the Introduction for some of the environmental and historical factors that may have influenced the observed patterns.) However, a few *suggestions* towards possible reasons for some of the observed patterns will be mentioned.

The patterns of areas with high levels of endemism at the genus level, as depicted in Fig. 4, appear more-or-less as expected, with the highest numbers of endemic genera occurring in the greater Cape Floristic Region (the core CFR + the Succulent Karoo). Also visible in the northeast are areas possibly including

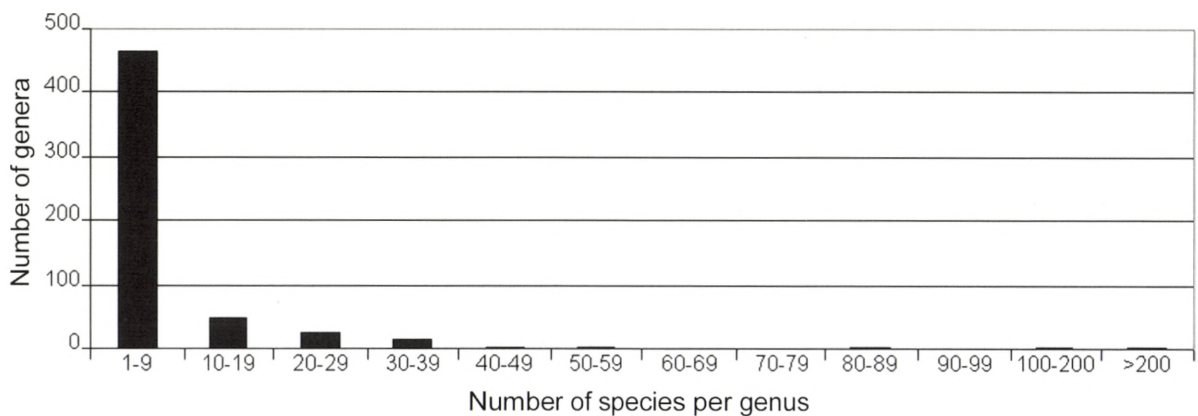


Fig. 3. Size distribution of genera endemic to southern Africa.

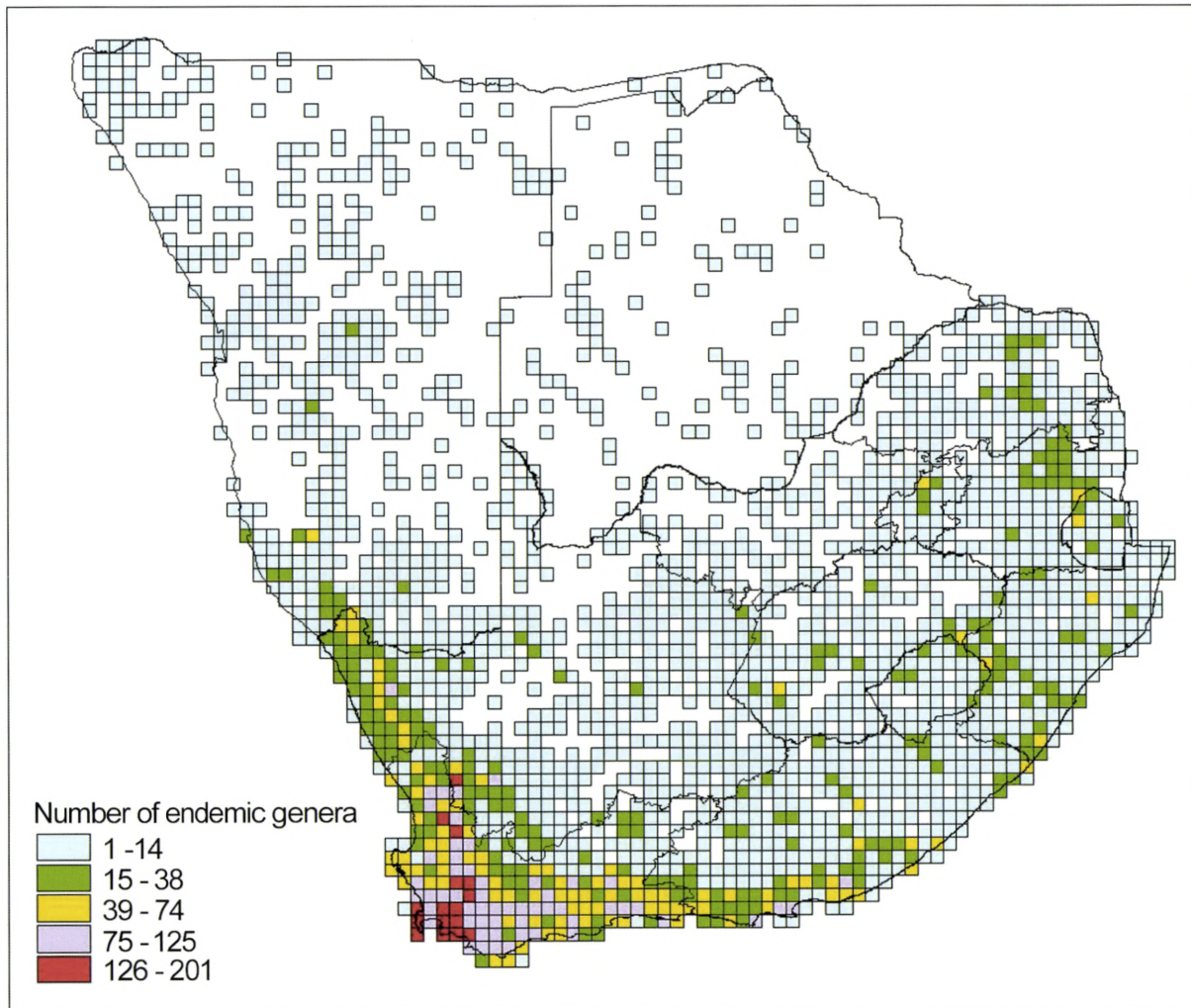


Fig. 4. Areas of high diversity for genera endemic to southern Africa.

the Soutpansberg, Wolkberg, Sekhukhune-land, and Barberton Centres of Endemism (compare Fig. 1). Along the east coast the small but significant Pondoland Centre of Endemism can be observed right at the border between KwaZulu-Natal and Eastern Cape Province. Further south, the Albany Centre appears more-or-less continuous with the greater Cape Floristic Region. Indications of higher levels of diversity in the interior (darker green spots), e.g. around Windhoek

(Namibia) and Pretoria (Gauteng), probably reflect artifacts of collecting intensity. Also see Fig. 5 for a map depicting PRECIS records of collecting intensity at the specimen level in southern Africa. Note the sparsely collected Karoo, Kalahari, and Namib regions – the high number of undercollected grids in these areas will have had an influence on the numerical classification discussed below, although this will not be significant due to the lack of local endemism in these extensive regions.

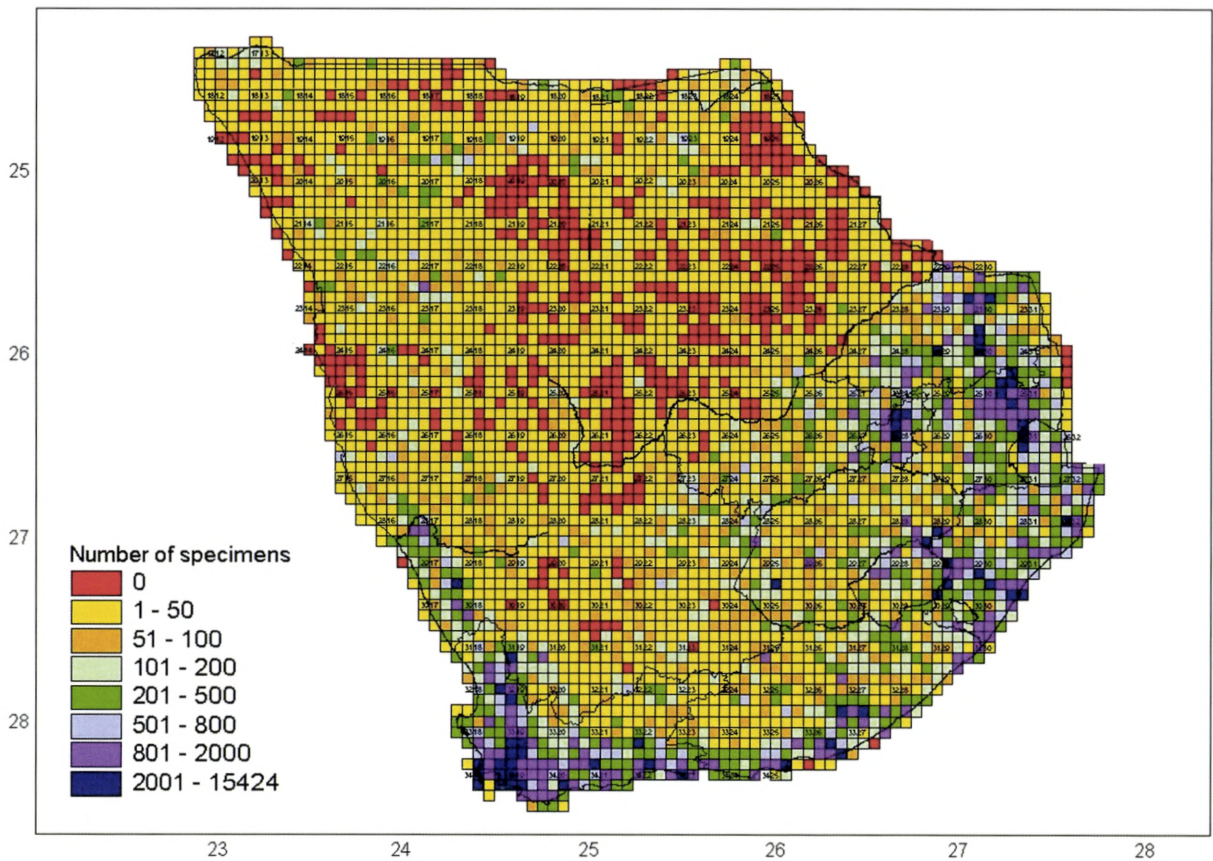


Fig. 5. Collecting intensity at the specimen level in southern Africa according to PRECIS records, indicating areas that are less well represented in the dataset used, and that could potentially influence the results of the numerical analysis.

The size distribution of seed plant genera endemic to southern Africa illustrated in Fig. 3 shows a clear bias towards smaller genera. This, together with the fact that 205 genera (34.9% of the total number of endemic genera) are monotypic, suggests that we are dealing with a relatively old and stable flora in southern Africa. The assumption is that most of the monotypic genera so prevalent in the southern Africa flora are palaeoendemics – relicts of ancient floras and taxa that covered the sub-continent – with no or few close extant relatives. However, even if most are not palaeoendemics, but neoendemic offshoots from other

taxa, one can still reason that it probably takes a long time for a taxon to develop to the point that it can be recognised as a separate genus, therefore still signifying an old flora. Both the high levels of floristic diversity and endemism, and the high numbers of monotypic genera in southern Africa, might be explained, at least partly, by the absence of any recent extensive glaciations in the region.

We suggest that the separation of the Kaokoveld phytocorion from the rest of the region at an early stage in the hierarchy (Figs 6, 7) may be taken as evidence confirming the hypothesis that this region is an ancient arid

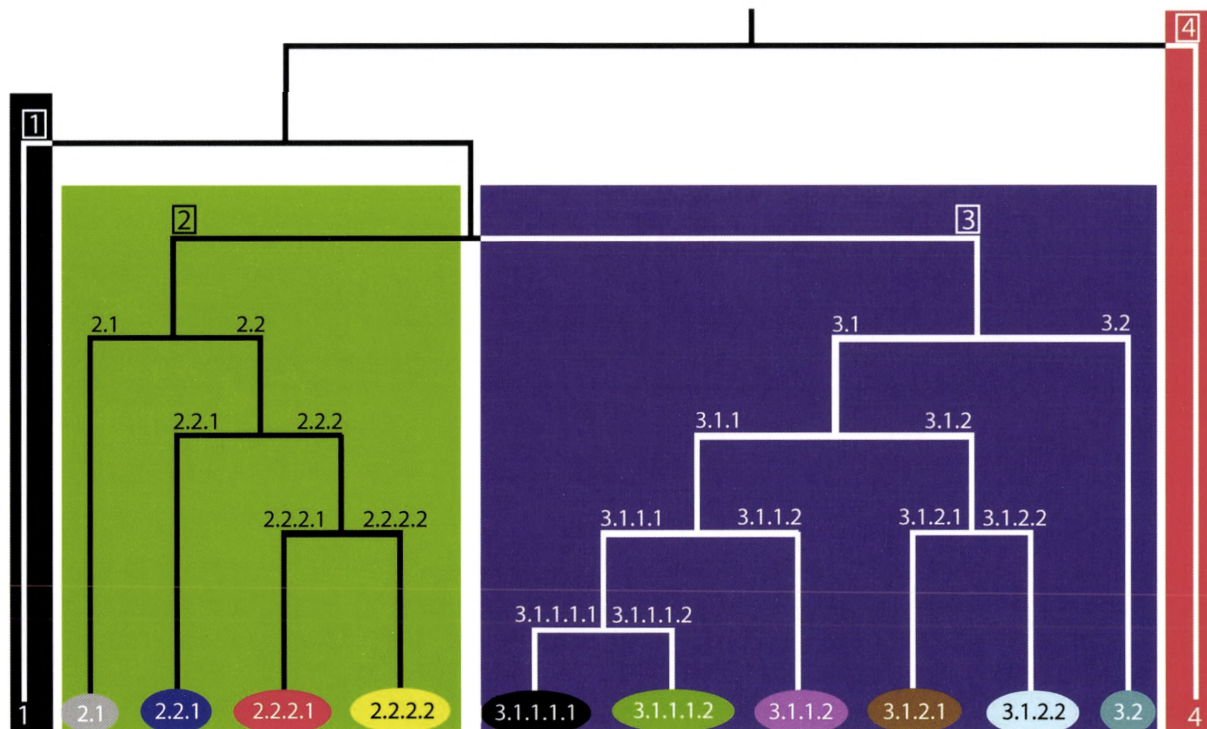


Fig. 6. Simplified dendrogram of the TWINSPLAN classification indicating a hierarchy of phylogeographic regions in southern Africa. Coloured rectangles in the background correlates with the colours used in Fig. 7, and indicate the higher level phytochoria of the hierarchy. Coloured ovals surrounding the numbers of the end-groups correlate with the colours used in Fig. 8, and indicate the lower level phytochoria of the hierarchy.

area, containing many relicts of earlier floras that has no or little connection to the other floras represented in this study, and that we should seek its relationships elsewhere. The boreotropical hypothesis (Wolfe 1975; Lavin & Luckow 1993; Xiang & Soltis 2001; Davis *et al.* 2002) may offer an explanation for this region's uniqueness. This hypothesis suggests that northern high-latitude land bridges, e.g. the Beringian bridge during the Tertiary and the North Atlantic bridge during the Eocene, may have served as migration routes for currently intercontinentally disjunct plant groups (Davis *et al.* 2002). This hypothesis may well be implicated to explain some of the disjunct distribution patterns between arid parts of southwestern Africa (e.g. Namibia) and the Ameri-

cas. Postulated ancient arid connections between the Horn of Africa and the Kaokoveld region (de Winter 1966, 1971; Verdcourt 1969; Thulin 1994; Jürgens 1997; van Wyk & Smith 2001) may have provided a link with the boreotropical flora. It is also possible that the Kaokoveld flora represents relicts of an ancient, arid, pre-Gondwana-breakup, flora (van Wyk & Smith 2001). Whatever the floristic relationships of the Kaokoveld region, it is clearly not with the Cape flora from further south in southern Africa, nor with the rest of the palaeotropical flora of the FSA region.

We would like to suggest that the split off of the Kalahari region from the main body at the second level of the hierarchy (Figs 6, 7) indicates that, like the Kaokoveld, the main rela-

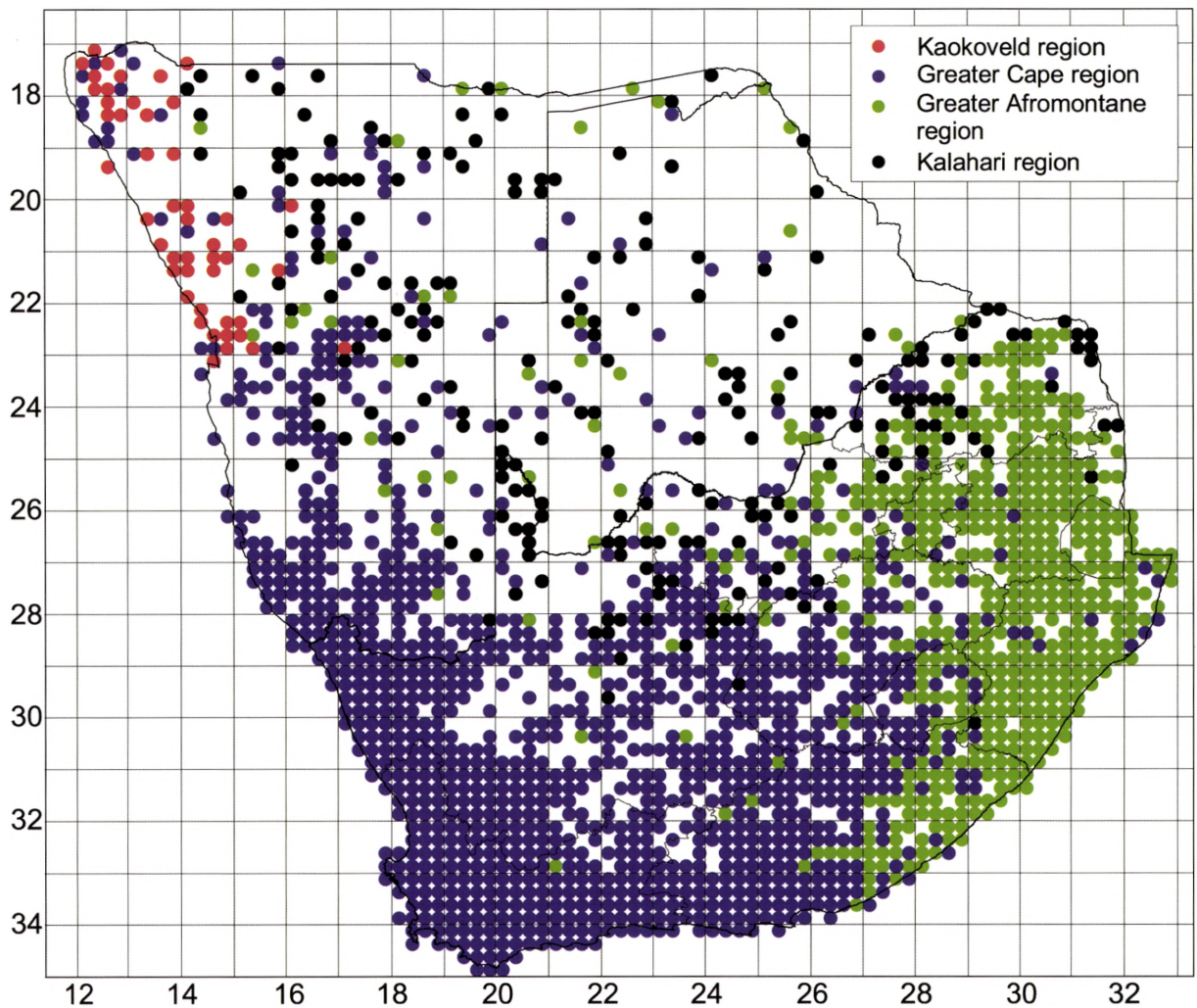


Fig. 7. Map illustrating the higher level phytochoria identified by the TWINSpan classification.

tionship of the Kalahari does not lie with the Cape flora. It is undeniable that the Kalahari region does share taxa with some of the southern regions, especially the Highveld grassland, but the fact that its endemic genus component distinguish it at an early stage from the southern phytochoria, suggest that its main relationship lies elsewhere. It is probable that this main relationship lies to the north, with tropical Africa, as the larger Kalahari region extends up to the Democratic Republic of the Congo. It is

often assumed that the uniqueness of the southern Kalahari is to be explained by its aridity. However, we would like to suggest that this is not the case. It is not so much its aridity, but the substrate upon which it occurs that determine the uniqueness. The Kalahari sand deposit, the largest deposit of windblown (aeolian) sand in the world, larger even than the Sahara Desert sand deposit, is probably a determining factor. It has been noted that the Kalahari sand deposits have a remarkable water

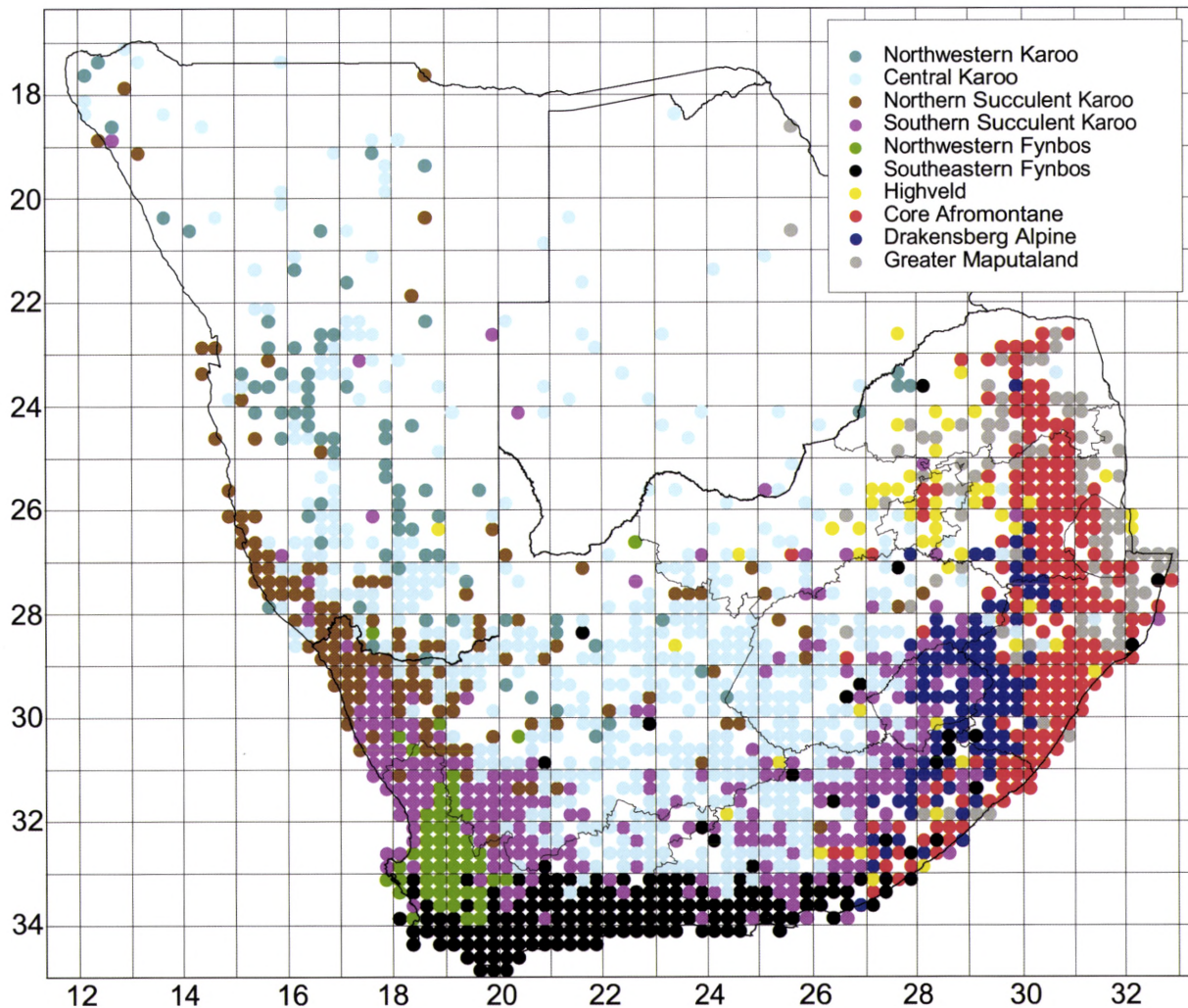


Fig. 8. Map illustrating the mid-level phytochoria identified by the TWINSpan classification.

infiltrating capacity, with very little runoff, a fact clearly reflected by the lack of drainage channels in the region. On the other hand, the clay soils of the Karoo lying just south of the Kalahari are characterised by poor water infiltrating capacity and high runoff. This would also explain the pattern we see in Fig. 7; that the Kalahari phytogeographical region extends into parts of the North-West, Limpopo and Mpumalanga Provinces of South Africa, where several outlier Kalahari sand deposits occur.

The second and third main groups of the hierarchy (Figs 6, 7) represent the Greater Afromontane and Greater Cape phytochoria respectively. It is noteworthy here that the line separating these two phytochoria runs more-or-less through the middle (north-to-south) of Lesotho. The Drakensberg Alpine region (van Wyk & Smith 2001) lies mostly on the higher eastern parts of the Lesotho mountains, and is, in our results (Fig. 7), clearly included in the Greater Afromontane region, and not the

Greater Cape region. This would seem to refute the suggestion made by previous authors (for example Linder 1990, 1994) that the Afroalpine (of which the Drakensberg Alpine forms part) region and the Cape region are closely related to each other, with the Cape region merely a regional specialisation within the larger Afromontane-Afroalpine region. Other hypotheses may explain the presence of Cape phytogeographic (floristic) elements on these high mountains. One explanation for the presence of the Drakensberg-Cape floristic link may be a result of the cyclic fluctuations of warmer and colder climates. During warmer times, the cold-adapted flora of the high Drakensberg Alpine region goes largely extinct, as there are no other high mountains nearby where it can take refuge. When the climate becomes more temperate again, there are, similarly, no nearby temperate refuges from where the Drakensberg Alpine's flora can be replenished, *except* for the Cape Floristic Region in the south. The floristic link between the Cape and the Drakensberg Alpine Regions does therefore not mean that the Cape is merely an extension of the larger Afromontane-Afroalpine phytochorion of Africa, especially not when one considers that the floristic composition of the far northern Afroalpine areas in Africa differs considerably from that of the southern Drakensberg Alpine region. The floristic link between the Cape and Drakensberg Alpine grasslands is instead a secondary manifestation as a result of relatively recent climatic variations, and reflects the ecotonal status of the Drakensberg as an interface between the Cape and non-forest Afromontane flora.

The Greater Maputaland region (2.1) (Figs 6, 8) is significantly smaller than the Maputaland-Pondoland Region of van Wyk & Smith (2001) (Fig. 1). The reason for this discrepancy is that the Maputaland-Pondoland Region of van Wyk & Smith (2001) is a convenient, and not a natural, classification and demarca-

tion. It includes not only the Maputaland and Pondoland Centres of Endemism (Fig. 1) but also the Afromontane region of the KwaZulu-Natal Midlands below 1,800 m a.s.l. The smaller area we identified in this study as the Greater Maputaland region is a more natural classification and demarcation. It is probably colder versus warmer climatic conditions that differentiate the Drakensberg Alpine (2.2.1) from the rest of the Afromontane region. The Highveld (2.2.2.2)-Core Afromontane (2.2.2.1) split distinguishes between the drier and colder (in winter) plateau on which the Highveld is located and the wetter and more humid escarpment and coastal areas in which the Core Afromontane occurs. What is noticeable is that at this level of the hierarchy, where the classification has been terminated, the Greater Pondoland region of southern KwaZulu-Natal and northeastern Eastern Cape Province, has not yet split off from the Core Afromontane region, even though it is known to be a strong centre of endemism (van Wyk & Smith 2001). This suggests a very strong relationship between the Pondoland Afromontane area and the Escarpment (including KwaZulu-Natal Midlands) Afromontane – a link previously indicated by van Wyk (1990). From this classification it appears that the Greater Maputaland region extends only as patches located in the larger, hotter river valleys (e.g. the Tugela River valley) into the Pondoland region. It is possible that the resolution we chose, namely quarter-degree grid squares, had an influence on this observed pattern.

It is noteworthy that in the further subdivision of the Greater Cape phytochorion, it becomes clear that the Northern Succulent Karoo (3.1.2.1 – almost identical to the Gariep Centre of van Wyk & Smith (2001)) is apparently more closely related to the Central Karoo (3.1.2.2) than to the Southern Succulent Karoo (3.1.1.2), which, in turn, appears to be more closely related to the Fynbos (3.1.1.1).

This might be an artifact of the fact that the resolution in this study are not truly fine enough to clearly distinguish between the Succulent Karoo and Fynbos areas within the strict Cape region. Especially in the Southeastern Fynbos, enclaves of Succulent Karoo, e.g. the Little Karoo and Worcester-Robertson Centres of van Wyk & Smith (2001), and Fynbos forms a mosaic at very small intervals. Enclaves of the Southern Succulent Karoo also appear in the southwestern high Karoo, southwest of Lesotho. The last subdivision between the Southeastern (3.1.1.1.1) and Northwestern (3.1.1.1.2) Fynbos regions can probably be explained by the orientation of the mountains in the area. In the Southeastern Fynbos, the mountains have a more-or-less east-west orientation (north-south aspect), while in the Northwestern Fynbos exactly the opposite occurs, with the mountains having a primarily north-south orientation (or east-west aspect). It is also colder and wetter in the Northwestern Fynbos region.

Conclusion

It can be concluded that numerical classification techniques, and specifically the computer program TWINSpan, show considerable potential for use in broad scale phytogeographic studies in southern Africa, and especially for the production of a formal hierarchical classification of the natural phytogeographic (floristic) regions of the area. PRECIS, in view of its current limitations in terms of data reliability (there is no measure in place to estimate the accuracy of the data) and in terms of data sufficiency (large areas of the study area are still underrepresented in PRECIS), exceeds our expectations in providing the basis for such large-scale, numerical classification-based, phytogeographical studies. The classification and maps obtained in this study com-

pare favourably with previously produced classification and maps, but some intriguing patterns, and especially relationships among the various phytochoria, became evident in this study.

Future studies

A definitive future project would be the rerun of this study using species in stead of genera. It is our opinion that such an analysis would not alter the patterns obtained in this study significantly, but that it would rather refine and add definition to these patterns. Two other investigations that would seem imperative would be the use of *all* genera and *all* species in two separate reruns of this study, so that one can compare the results from studies using all native taxa to those using endemic taxa.

We also foresee that the use of different sample-grid sizes, for example half-degree grid squares instead of quarter-degree grid squares will also need testing, as the sample-grid size would affect the clarity and definition of the biogeographical patterns obtained.

Since the use of a divisive numerical method proved very useful and informative in producing biogeographical interpretable results, it seems somewhat of a wasteful luxury to redo the study using an agglomerative method. However, it might prove informative to compare the results from such a study – using an agglomerative method – with the results obtained in this study.

Biogeographical and taxonomic studies designed to test the hypotheses we suggested in this paper, as possible explanations of the observed biogeographical patterns should also be carried out. Of special interest here is the suggestions we made with regard to the Kaokoveld and Kalahari regions that were identified in this study.

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