South African Journal of Botany 2003, 69: 1–10
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SOUTH AFRICAN JOURNAL
OF BOTANY
ISSN 0254–6299

Nama-karoo veld types revisited: a numerical analysis of original Acocks' field data

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Received 15 November 2002, accepted in revised form 28 November 2002

This paper assesses Acocks' veld types against a reclassification of his own data for the Nama-karoo using a suite of multivariate techniques. The analysis showed that the vegetation of Nama-karoo can be partitioned into three major clusters with the most clearly defined cluster corresponding to areas in the arid north-west. Within these clusters the species groups or *pools* substantiated a number of Acocks' veld types and some of their subdivisions. Notable in this regard are the veld types Orange River Broken Veld and Arid Karoo as well as some of their subdivisions. The findings suggest that some of these subdivisions could well have been raised to full veld type status. Also confirmed was the nebulous nature of Central Upper Karoo and False Arid Karoo with gradual transitions to most neighbouring veld types.

Not supported by the analysis are False Succulent Karoo and several veld types, or parts of veld types in the south-eastern Nama-karoo. Non-coincidence with the units of the numerical analysis in the latter area may also be a consequence of a mismatch between Acocks' large sample areas and his relatively fine mapping scale in this particular region.

Introduction

John PH Acocks devoted most his working life to surveying and characterising the vegetation types of South Africa and this work is probably still the most cited published work on the vegetation of South Africa (Cowling 1999). He termed his vegetation units veld types which, although he defined these as having the 'same farming potentialities', he also emphasised how, for practical purposes, he used about 2 000 'more or less important' species for his classification in 1953. His vegetation map and subsequent hierarchy was an intuitive, expert-based system. His veld type descriptions clearly show a floristic approach at the species level. He also introduced the concept of 'False' veld types that he indicates have changed from previously different types due to anthropomorphic influences.

Acocks did not sample the country evenly, or in proportion to its plant diversity. For example, large areas of the Kalahari and of the Limpopo Province were not sampled (Rutherford *et al.* 2003). This was due to insufficient time and sometimes to difficulties of access. However, one biome that he surveyed intensively and resided in for most of his life was what is now recognised as the Nama-karoo Biome (Rutherford and Westfall 1994, Low and Rebelo 1996).

In view of the considerable influence that Acocks' work has had on South African ecology and biogeography over several decades (Cowling 1999), this paper assesses Acocks' veld types against a reclassification using a suite of multivariate methods that use his own data sets for the Nama-karoo. Acocks did not have access to these methods for his seminal work that appeared in 1953. Indeed, very few ecologists worldwide had applied such quantitative classification techniques to large data sets in an era where computer technology was still in its infancy and unavailable to most. Acocks continued to sample areas in South Africa after 1953, more than doubling (131% increase) the number of sites in the Nama-karoo (Rutherford *et al*. 2003). Following his final sampling, Acocks revised his veld types of the semi arid to arid western half of the country (Acocks 1979). Some of his revisions were published as an Addendum in Acocks (1975). The addendum was omitted without incorporation of the changes in the text in Acocks (1988). In 1977 he provided a useful list of veld types with variations (Acocks 1977) which were not as clearly expressed in Acocks (1979). In these unpublished documents (held by the National Botanical Institute) he does not provide a new map for this area but he does indicate where he deemed changes to the map should be made. The number of changes is surprisingly few given that the map was based on less than half his final data set. Most of the revision concerned expanding the descriptions of the veld types. In this follow-up work, he did not apply any formal classification technique and relied on inspection of tabulated frequencies of occurrence of what he considered 'important' species per site (usually several hundred species per veld type). The status of his 'false' veld type units is also examined in the light of the new analysis.

Materials and Methods

Data source

The original data for Acocks' sampling sites were computerised (and names updated) by the National Botanical Institute to form a database known as ACKDAT (see O'Callaghan 2000; Rutherford *et al.* 2003). His estimates of abundance of individuals of each species are also captured in the database. Only sites where it was apparent that species had been comprehensively recorded were included. The total number of species included in the analysis for Nama-karoo was 2 629 in 1 085 sites, which included 39 sites in the adjacent southern Nama-karoo of Namibia (south of 26°S and east of 18°E). Nama-karoo was defined according to Low and Rebelo (1996) for South Africa and according to Rutherford (1997) for Namibia, and was slightly modified at some edges of the biome to be more inclusive, particularly towards the Roggeveld escarpment and some arid upland areas between Aberdeen and around Hofmeyer. The marginal Noorsveld and narrow belts of Spekboomveld of the escarpment that interdigitate with Nama-karoo were also included. Although some veld types extend beyond the Nama-karoo biome (e.g. Western Mountain Karoo) only those parts within the biome are considered. Of the 15 veld types that occur in the Nama-karoo, seven are regarded as false types by Acocks.

Data transformation and collation

The original Acocks' data were species abundance counts showing a broad range of values (1 to 15 122 520 individual plants per hectare (Killick 1975)). In order to remove an artefact resulting from Acocks' peculiar way of determining abundance (without proper relation to sample size involved), we transformed the original large-span scale into a simple 0–8 ordinal scale (0: for non-occurrence; increasing score indicates higher class of abundance span) as follows:

Transformed abundance = 1+Integer
(Log([Abundance Value])/Log(10)*10+0.5)/10

Pre-classification procedures

The transformed data were imported into the National Vegetation Database (Mucina *et al.* 2000) in TwWin2.0 format (Hennekens and Schaminée 2001) to assure flexible data-export options. A data matrix containing the Acocks' samples pertinent to the Nama-karoo region was then created to fit the format of the Megatab2.0 package (Hennekens 1996). Megatab2.0, which is a part of the TvWin2.0 (Turboveg) package was designed to handle basic shuffling procedures with phytosociological tables, and includes a number of formalised programs aiding construction of sample tables, synoptic tables, computations of resemblance, and of internal homogeneity of clusters/pools, as well as manual shuffling of species and/or relevés. TWINSPAN (Hill 1979) is one of the major tools imbedded within Megatab2.0. It is incorporated here in a special version allowing for analyses of partial tables within the handled data set.

A series of iterative steps involving global TWINSPAN analyses (including all Acocks' samples), and local analyses (limited to parts of the handled table) were performed. The primary aim of this procedure is the refinement of a classification to avoid known drawbacks of TWINSPAN. These are rooted in a tendency for mis-classification of samples situated in the centre of the horse-shoe pattern in the underlying ordination using correspondence analysis.

In summary the initial sorting of the total data set included the following steps:

(1) TWINSPAN on total data set with selected pseudo-level functions preserving the original 0–8 scale,
(2) probe into internal homogeneity of the resulting groups of samples and decisions (aided by internal homogeneity, synoptic table) on retaining them or new partial TWINSPAN analysis,
(3) repetition in Steps 4 and 6 until final sample-group pattern was established.

Using this procedure, the sampling universe of the original Acocks' field samples was subdivided into 45 relatively homogeneous sample-groups, here termed *pools*. We prefer to use this term rather than 'clusters' since the resulting group was derived using a divisive (pooling) technique (see Pielou 1984). The clusters are a result of clustering (amalgamation) procedures.

Clustering and ordination of resultant pools

In order to investigate the resemblance patterns in clustering and ordination spaces among the 45 pools we employed Complete Linkage Clustering (CLC) for the hierarchical classification and Principal Coordinates Analysis (PCO) for ordination.

CLC was selected for its effectiveness in conserving resemblance space. The choice of the Chord Distance as resemblance was lead by the uneven total number of species in particular species vectors characterising the pools (the number of original samples for pools varied, hence also the species richness per Pool varied considerably). The differences in species richness can be remedied by species vector normalisation — a type of vector transformation. Chord Distance is equivalent to the well-known Euclidean Distance incorporating normalisation (for theory consult Podani 1994, 2001).

Principal Coordinate Analysis (Gower 1966, 1987) is a scaling technique (Podani 1994), and unlike PCA or Correspondence Analysis (or is derivations), allows using of practically any kind of resemblance. We used again Chord Distance as the resemblance to be able to compare the clusterings and ordinations directly. The ordinations served to identify the derivation of floristic coenoclines in the data, and to visualise the resemblance patterns.

The computations were performed using the program package SYNTAX 2000 (Podani 2001).

The resultant pools (as well as clusters resulting from cluster analysis of the pools) were used to evaluate Acocks' veld types units as mapped in 1953 but including the few modifications indicated in 1979. The number of sites belonging to a given pool within a veld type was analysed relative to the total number of sites in the pool. To avoid an unduly restrictive interpretation of Acocks' intent in an era of hand mapping with poor availability of spatially explicit environmental data layers, we relaxed his boundaries by 20km. This gives a more reasonable indication of degree of congruence between a pool and veld type. Where data are used across a common veld type border, the 20km buffer was excluded to avoid counting the same site more than once. Although buffering of veld type boundaries provides useful insights in most of the Nama-karoo, where the landscape and veld types are more finely dissected (especially in the south-eastern parts of the Nama-karoo) buffering becomes less useful.

The approach used in interpreting the pool patterns followed the following principles: Where, for example, a buffered veld type had a reasonable representation of given sites (say at least 15) and this also represented a high proportion (say at least 85 %) of all the sites of the pool, this pool would help justify the unit as a veld type. Multiple such pools within a veld type would more strongly support the recognition of that veld type. A larger number of poorly represented pools in a veld type would reduce its chance of substantiation. Highly divergent pools inter-dispersed within the same veld type may indicate a mosaic of habitats or the inclusion of azonal communities in the sample site.

Results and Discussion

Numerical analysis of Acocks' field data

A pre-classification of the Acocks' field samples resulted in 45 pools with an average size of 24 sample sites (Table 1). A cluster analysis of the 45 pools (Figure 1) revealed three large clusters (A, B, and C) in the data set. The first-order dichotomy (cluster A and clusters B and C) reflects the west-east climatic ecocline paralleled by a coenocline revealed by a PCO. The ordination diagram (Figure 2) reveals a clear (convoluted) horseshoe effect. Cluster A features on the positive (Axis 1) branch of the coenocline, while clusters B and C share the negative (Axis 1) branch. This coenocline as well as the dichotomy revealed by the cluster analysis, suggests dividing the Nama-karoo into two subunits. For the purposes of this paper we refer to the Cluster A subunit as 'arid' (mean annual rainfall 50mm to 250mm, mean annual potential evapotranspiration 2 600mm to 2 900mm) and the other clusters as 'semi-arid' (mean annual rainfall 100mm to 450mm, mean annual potential evapotranspiration 2 200mm to 2 700mm) (Schulze 1997).

Cluster A separates clearly from the rest of the data set. It is comprised of samples from the western parts of the region encompassing mainly Acocks' veld types Arid Karoo, False Arid Karoo, Orange River Broken Veld. Following the structure of the Acocks' field data, the species limited to this cluster include:

shrubs and sub-shrubs: *Acacia hebeclada, Ceraria namaquensis, Curroria decidua, Euphorbia gariepina,*

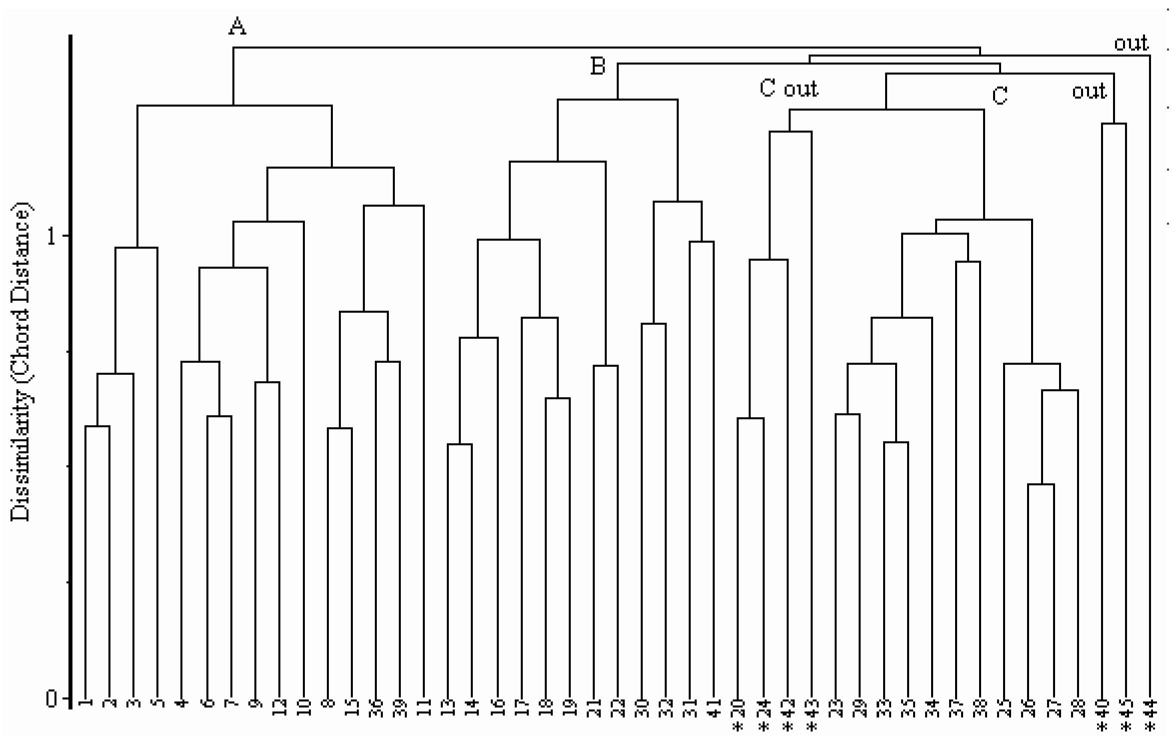

Figure 1: Dendrogram of Complete Linkage Clustering (using Chord Distance as resemblance) of 45 sample-groups (pools) resulting from a series of TWINSPAN analyses of the original Acocks' Nama-karoo data set. A, B, and C indicate the clusters. The asterisks indicate outlier pools

Table 1: Percent of sites for each pool[a] that occur inside, and within 20km, of the corresponding Acocks (1953) Veld Type

Pool	Pool size (number of sample sites)	29 Arid Karoo	32 Orange River Broken veld	35 False Arid Karoo	36 False Central Upper Karoo	39 False Succulent Karoo	40 False Orange River Brokenveld	27 Central Upper Karoo	26 Karroid Broken Veld	28 Western Mountain Karoo	30 Central Lower Karoo	37 False Karroid Broken Veld	38 False Central Lower Karoo	25 Spekboomveld	24 Noorsveld	42 False Karoo replacing Karroid *Merxmuellera* Mountain Veld
1	25		**90**[b]													
2	45	35	70			18										
3	30	43	71		7											
5	14		100													
4	26	65	**100**[b]				4									
6	32	**100**[b]	84			6										
7	38	63	37	34	3		19				5					
9	7	100		14												
12	39	**95**[b]				18				21						
10	32	**93**[b]		3	3	53				7						
8	31	32	13	71	19		11	29		6	3					
15	46	43		46	17			50	9	17	4					
36	17			35	76			18				35				
39	14		7	50	71			14								
11	8		88	25	13											
13	30	**90**[b]						10							3	
14	46	17		39	17			67	17		11					
16	23	70						17	9	**87**[b]						
17	9		11		11				78							
18	36				8			31	**92**[b]		28					
19	43				19			12	74		79	26	12			
21	20	25		25	20			50	30	5	10	5				
22	22	36		27	23			45			5					
30	22				**86**[b]						9	55	27			18
32	15				80			20								13
31	5				80											
41	3							100								100
20	23								**91**[b]		78		39	**96**[b]		4
24	49								35		45	76	65	**86**[b]	47	
42	10								50			70		80	50	20
43	7													33		50
23	22			23	73			14			18					
29	84				**94**[b]			4			1	12				7
33	23				83			9	13		9					
35	24				**96**[b]			33								
34	2				100											
37	11			18	45			55								
38	26				**92**[b]							4				
25	18				56			17				39				56
26	59				**88**[b]							32	17			
27	24				67			21	21			63		25		
28	8				38							75	63			63
40	8	63								100						
45	4				50											50
44	5								40		40	100	100			

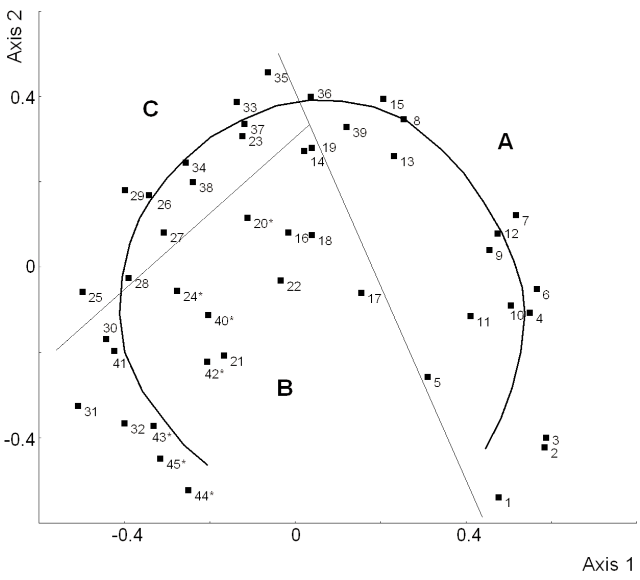

Figure 2: Ordination diagram (Axes 1 and 2) of Principal Coordinate Analysis (using Chord Distance as resemblance) of 45 sample-groups (pools) resulting from a series of TWINSPAN analyses of the original Acocks' Nama-karoo data set. A, B, and C indicate the clusters of the clustering analysis. The asterisks indicate the pools of outlying properties

Hermannia abrotanoides, Kissenia capensis, Leucosphaera bainesii, Lycium bosciifolium, Pergularia daemia, Sisyndite spartea, Zygophyllum dregeanum, Z. gilfillanii;
herbs: *Aizoon asbestinum, A. schellenbergii, Aloe hereroensis, Aptosimum albomarginatum, A. lineare, Barleria lancifolia, B. lichtensteiniana, Blepharis mitrata, Chascanum garipense, Coccinia rehmannii, Codon royeni, Corchorus asplenifolius, Cucumis sagittatus, Cyamopsis serrata, Dipcadi glaucum, Garuleum schinzii, Geigeria pectidea, Indigofera auricoma, I. heterotricha, I. holubii, Lotononis rabenaviana, Monsonia umbellata, Oxalis lawsonii, Tribulus cristatus, T. pterophorus*;
grasses: *Centropodia glauca, Eragrostis echinochloidea, Eragrostis brizantha, Stipagrostis uniplumis* var. *neesii, Triraphis ramosissima*;
and trees: *Acacia erioloba, Aloe dichotoma, Boscia foetida* subsp. *foetida* and *Parkinsonia africana*.

Cluster B shows less consistency with the Acocks' veld types (see Table 1 with pools grouped into clusters according to Figure 1). However, many samples falling within the polygons of the Karroid Broken Veld, Central Upper Karoo, south-eastern parts of the Western Mountain Karoo, and False Central Upper Karoo (formerly False Upper Karoo) coincide with this cluster. The cluster is heterogeneous. Only diagnostic species such as *Chrysocoma oblongifolia, Indigastrum costatum* subsp. *macrum, Ehrharta pusilla* and few others occur throughout cluster B. At least two distinct sub-clusters can be recognised. One of them comprises pools 18 and 19 in the Great Karoo. The diagnostic species found in this sub-cluster include *Moraea marlothii, Asparagus fasciculatus, A. multituberosus, Ursinia pilifera, Hesperantha radiata, Androcymbium volutare, Pharnaceum croceum, Merxmuellera dura* and *Drosanthemum ambiguum*. The other sub-cluster is composed of pools 30, 31, 32 and 41 and is dispersed towards the north-east of the biome. Diagnostic species of this sub-cluster include *Aloe tenuior, Hermannia gracilis, Pappea capensis, Viscum obscurum, Euphorbia coerulescens, E. esculenta, E. heptagona, Crassula ovata, Zygophyllum foetidum, Ruschia parviflora, Asparagus subulatus, Sporobolus nitens, Schotia latifolia, Pelargonium peltatum, Polygala myrtifolia* and *Encephalartos lehmannii.*

Cluster C is mainly limited to the eastern part of the biome. Its diagnostic species include: *Dianthus thunbergii, Sporobolus discosporus, Euryops empetrifolius, Rhus ciliata, Nolletia ciliaris, Crassula dependens, C. lanuginosa, Selago brevifolia, Cymbopogon excavatus, C. prolixus, Helichrysum niveum, Eragrostis superba, Euclea crispa* subsp. *ovata, Hermannia glabrata, Adromischus nanus* and *Aristida canescens*.

Cluster C coincides mainly with False Central Upper Karoo and veld types characteristic of regions now included in the Thicket Biome (Low and Rebelo 1996), such as Noorsveld and Spekboomveld (see Table 1 with pools grouped into clusters according to Figure 1). Other veld types associated with cluster C are marginal to the Nama-karoo, being located in the south-east of the biome where they are adjacent to the Thicket and Grassland Biomes (Central Lower Karoo, False Central Lower Karoo, and False Karroid Broken Veld). This is reflected in the emergence of a cluster (designated as 'C out': Figure 1) which, together with the outlying pools 40, 44 and 45, render the clear separation of clusters B and C problematic. Using environmental data, Palmer and Hoffman (1997) also derive three distinct regions within the Nama-karoo. Their Griqualand West and Bushmanland region corresponds closely to cluster A while their remaining two regions confirm the complexities of distinguishing between clusters B and C.

There are a high number of semi-desert generalists which occur with equal frequency in both arid and semi-arid parts of the Nama-karoo and which emphasise the overall 'homogeneous' character of the vegetation of the biome. These include:
shrubs: *Chrysocoma ciliata, Eriocephalus ericoides, Felicia muricata, Gomphocarpus fruticosus, Lycium cinereum, L. prunus-spinosa, Pegolettia retrofracta, Pentzia globosa, P. lanata, P. spinescens, Plinthus karooicus, Pteronia sordida, Salsola glabrescens*;
grasses: *Aristida adscensionis, A. diffusa, Cenchrus ciliaris, Enneapogon desvauxii, Eragrostis homomalla, E. lehmanniana, Fingerhuthia africana, Stipagrostis obtusa, Tragus berteronianus, T. racemosus;*
and herbs: *Aptosimum elongatum, Berkheya annectens, Chamaesyce inaequilatera, Convolvulus sagittatus, Dicoma capensis, Indigofera alternans, Kohautia cynanchica, Lessertia frutescens*, *Leysera tenella, Melolobium candicans, Mollugo cerviana, Moraea pallida* and *Trichogyne paronychioides*.

Acocks' map of veld types revisited

Orange River Broken Veld

Acocks' (1979) revision extends Orange River Broken Veld (Variation 32.1, Table 2) from the Vioolsdrif area to beyond his 1953 eastern limit of Namaqualand Broken Veld to Kenhardt (Acocks 1975 Addendum) or to Upington (Acocks 1979). This new unit is well supported by the three closely allied species pools 1, 2 and 3. The unit includes 75% of the three pools taken together, or 88% if buffered. These pools also include almost all the sites in south-western Namibia. The remainder of this veld type (Variation (32.2)) east of Upington, which Acocks (1979) revised as transitional to the Vryburg Shrub Bushveld Variation of Kalahari Thornveld to the north (which lies outside the area of analysis), is well supported by the rather distinct pools 4, 5 and 11 (Figure 1). Whereas the area of this veld type west of Upington contains only one site belonging to another pool, the area east of Upington is more diluted with sites of other pools. This supports Acocks'(1979) recognition of the transitional nature of this section of the veld type. Our data suggest that this veld type is also transitional to the south. The numerical analysis vindicates Acocks' revision of his original veld types in this region. However, the western section of this veld type is so distinct from the eastern section that these could well have been made separate veld types. Owing to inadequate description of Acocks' sample sites in this area, it was not possible to separately analyse Variation (32.3a), which appears to be associated with the Arid Karoo margin to the south, and Variation (32.3b), which is most extensive in eastern part of the unit to the east of Upington. It appears that, in contrast to the first two variations that were described as geographical regions, the last two variations may reflect habitat types within the geographical regions. However, given the number of pools closely associated with these regions, it is possible that some of the pools characterising

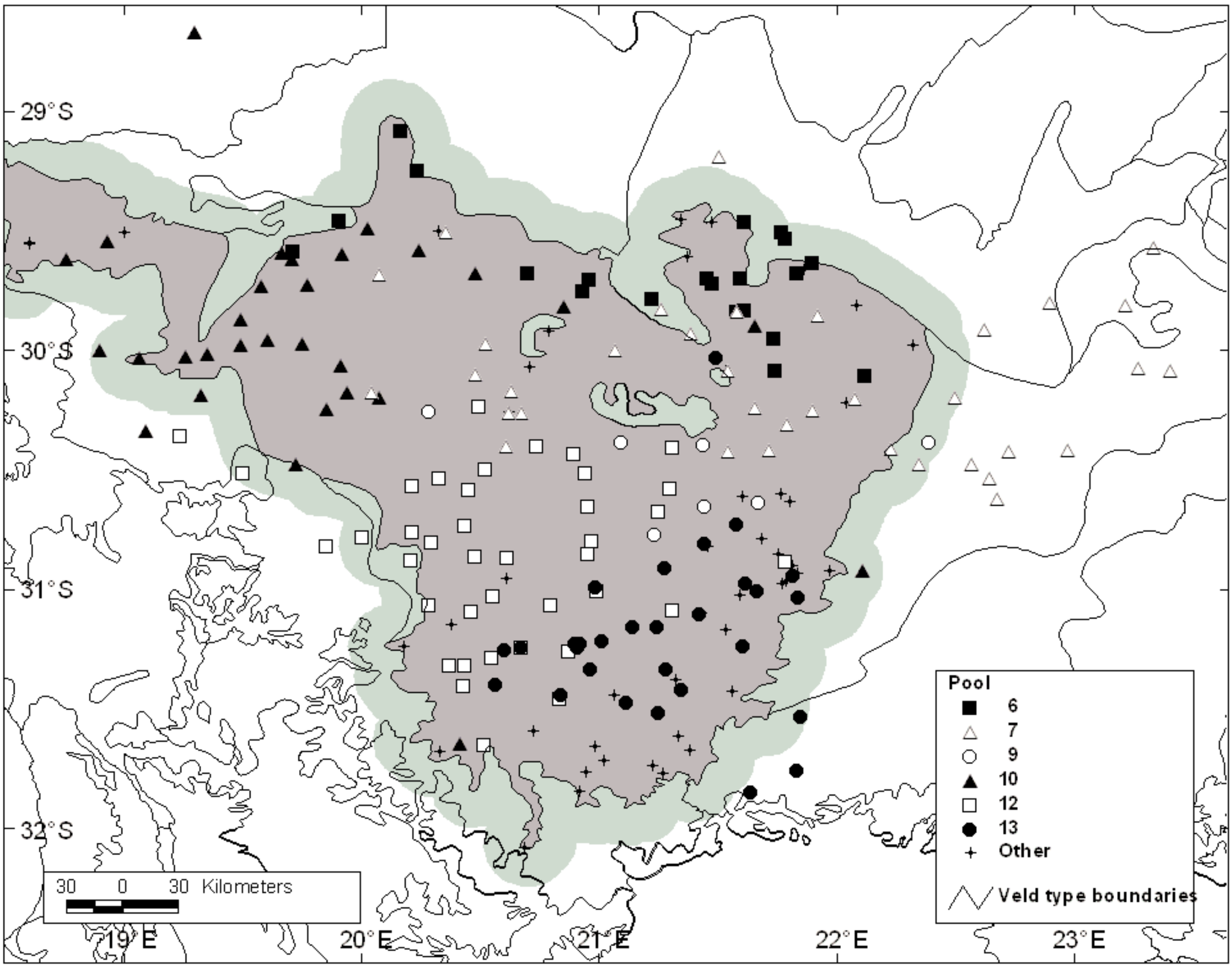

Figure 3: The veld type Arid Karoo (in dark grey) showing the six pools that each have a majority of sites within the veld type and also showing their occurrence outside the veld type. The other remaining sites in Arid Karoo are spread over 10 pools each with a majority of sites (ranging from 64% to 90%) outside the veld type. A few pool symbols are unavoidably obscured under others. The 20km buffer zone around the veld type is indicated in light grey

Table 2: Veld types of the Nama-Karoo with sub-divisions according to Acocks (1977)

Veld Type No.	Veld Type	Sub-division No.	Sub-division	Member of Nama- Karoo
24	Noorsveld			Marginal
25	Spekboomveld	25.1	North-eastern	Marginal
		25.2	Central	Marginal
		25.3	Western	No
26	Karroid Broken Veld	26.1	Little Karoo (including Robertson Karoo)	No
		26.2	Transition to Great Karoo	No
		26.3a	Great Karoo: West (Koup)	Yes
		26.3b	Great Karoo: Central	Yes
		26.3c	Great Karoo: East	Yes
27	Central Upper Karoo	27.1	Major hills	Yes
		27.2a	Rocky ridges and kopppies: West	Yes
		27.2b	Rocky ridges and kopppies: East	Yes
		27.3	Flats	Yes
		27.4	Vleis (Riverine vegetation)	Yes
28	Western Mountain Karoo	28.1	Upper (non-succulent)	Yes
		28.2	Lower (semi-succulent)	No
29	Arid Karoo	29.1(a)	Blomkoolgannaveld (western)	Yes
		29.1(b)	Blomkoolgannaveld (eastern)	Yes
		29.2(a)	Driedoringveld (western)	Yes
		29.2(b)	Driedoringveld (eastern)	Yes
30	Central Lower Karoo	30.1	West of Kariega river	Yes
		30.2	East of Kariega river	Yes
32	Orange River Broken veld	32.1	Typical [mostly Veld Type 33 in Acocks (1953)]	Yes
		32.2	Griqualand West	Yes
		32.3a	Transitional to Arid Karoo (Driedoringveld)	Yes
		32.3b	Swarthaakveld	Yes
35	False Arid Karoo	35.1a	South-western: flats and low ridges	Yes
		35.1b	South-western: Rocky hills	Yes
		35.1c	South-western: Rocky hills transitional to Orange River Brokenveld	Yes
		35.2a	Central: flats and low ridges	Yes
		35.2b	Central: Rocky hills	Yes
		35.3a	North-eastern: flats and low ridges	Yes
		35.3b	North-eastern: Rocky Hills	Yes
		35.3c	North-eastern: Kalk (Calcareous tufa flats)	Yes
36	False Central Upper Karoo	36.1a	South of Orange River: rocky hills	Yes
		36.1b	South of Orange River: flats	Yes
		36.1c	South of Orange River: vleis (Riverine)	Yes
		36.2a	North of Orange River: rocky hills	Yes
		36.2b	North of Orange River: flats	Yes
		36.2c	North of Orange River: vleis (Riverine)	Yes
37	False Karroid Broken Veld	37.1	ex Eastern Province grassveld of flats	Yes
		37.2	ex Eastern Province grassveld of mountains	Yes
		37.3	ex Spekboomveld	Yes
		37.4	ex Dry *Cymbopogon-Themeda* Veld of escarpment	Yes
38	False Central Lower Karoo			Yes
39	False Succulent Karoo			Yes
40	False Orange River Brokenveld			Only part
42	False Karoo replacing Karroid *Merxmuellera* Mountain Veld			Yes

This table presents data from Acocks (1977) except for data shown in round brackets, which are from Acocks (1979)

the western and eastern parts of this veld type may also support one or both of these last two variations.

False Succulent Karoo

The False Succulent Karoo is not supported by the numerical analyses. Instead, the floristic data suggest that it should be included with the Arid Karoo, except for a small area in the north that may form part of the Orange River Broken Veld. This veld type was not grouped with the Succulent Karoo Biome by Rutherford and Westfall (1994) but with the Nama-karoo Biome based largely on climatic correlations. Acocks (1953) does concede: 'This is a somewhat vague type' and in 1979 confirmed its relationship by stating 'it is derived from the Arid Karoo' to the east.

Arid Karoo
Acocks (1953) divides his large Arid Karoo veld type into three main variations, namely, Blomkoolganna Veld mostly along the northern edge of the plateau, Driedoring Veld mostly in the central part and a Semi-succulent Southern Form south of the Carnarvon-Calvinia road. Acocks (1979) has only two main variations and merges the southern form with False Arid Karoo. Pools 6 (in the east (Subdivision 29.1b)) and 10 (in the west (Subdivision 29.1a)) support his northern variation (Figure 3). A clear link with False Arid Karoo is indicated by pool 7 sites which also occur in the northern part of Arid Karoo and extend eastwards, mainly into False Arid Karoo (see Figure 3). The central variation corresponds to pools 9 and 12; the latter merges with a southern pool 13, which occurs just to the north and south of the Carnarvon-Calvinia road. It appears that Acocks (1979) could have retained his southern variation unit. He would also have been justified in at least raising his two main variations to veld type status.

Western Mountain Karoo
The analysis supports the Nama-karoo section of Western Mountain Karoo, which corresponds closely to pool 16 and also to pool 40, which extends into the adjacent Mountain Renosterveld veld type. This area of Western Mountain Karoo forms only part of Acocks' Variation 28.1 (Table 2).

False Arid Karoo
The False Arid Karoo is marginally supported by pool 8 but other pools indicate transitions to Arid Karoo (pool 7), Central Upper Karoo and False Central Upper Karoo (pools 36 and 39) and to Arid Karoo, Central Upper Karoo and False Central Upper Karoo (pools 14, 15 and 22). Even pool 8 overlaps into the last mentioned group. These pools are relatively heterogeneous and occur across much of the dissimilarity spectrum (Figure 1). Thus, while showing some gradual transition to Arid Karoo in the west, False Arid Karoo is also not a well-defined unit to the south and east. In 1953, Acocks acknowledged that the eastern boundary of this veld type is not clearly defined (where it meets with the Central Upper Karoo). This is consistent with his view that the original state of False Arid Karoo was Central Upper Karoo (Acocks 1953, 1979). In 1953, Acocks regarded the western boundary of False Arid Karoo as 'clearly defined' but later joined to it the southern variation of Arid Karoo (Acocks 1979). In 1979 he introduced three 'main subdivisions' of this type, namely south-western, central and north-eastern (Table 2). None of these subdivisions is supported by the numerical analyses.

Central Upper Karoo
The Central Upper Karoo veld type is not well supported by any pool. Pool 14, which is best represented in this veld type, would also support merging this veld type with False Arid Karoo, which, as stated above, Acocks (1953) regarded as being derived from Central Upper Karoo. In their simplification of Acocks' veld types, Low and Rebelo (1996) appropriately joined Central Upper Karoo and False Arid Karoo. Although Central Upper Karoo lies roughly central to some pools, these are diffuse and widely spread from south-eastern Arid Karoo to south-western False Central Upper Karoo. These pools (15, 21 and 22) also indicate affinity with False Arid Karoo. Two pools (36 and 39) also show a gradual transition to False Arid Karoo and False Central Upper Karoo. The floristic data do not agree with Acocks (1953) assertion that 'This is a well marked veld type'. His four main variations of this veld type are habitat- rather than locality-related.

False Orange River Broken Veld
Analysis of the few sites in the False Orange River Broken Veld (only the southern half is in Nama-karoo) does not indicate a floristic distinction from surrounding units. Acocks (1979) agrees that the unit is a meeting place of surrounding types (Orange River Broken Veld, Vryburg Shrub Bushveld and Karoo) but he asserts that the whole unit is a 'clear-cut veld type'.

False Central Upper Karoo
Acocks replaced the name False Upper Karoo with False Central Upper Karoo (Acocks 1979). False Central Upper Karoo is very well supported by pool 29 over almost its full extent (except the south-western part, around Richmond) and pools 33, 32 and 23 are similar in extent but less well represented. Pools 29, 33 and 23 are closely related (Figure 1). Pool 26 also covers much of the central and southern extent of the veld type but extends southwards on to a grassland unit (Karroid Merxmuellera Mountain Veld) and elsewhere. Pools 30, 27 and 25 better illustrate this gradient into the southern mountain grasslands. Pool 38 occurs exclusively north of the Orange River while pool 35 occurs well to the south of the river. This southern pool corresponds to that area of False Central Upper Karoo that Rutherford and Westfall (1994, Figure 15) contended — on climatic grounds — was not a false type (derived from grassland), but a karoo type proper. The last mentioned two pools certainly highlight the floristic differences along the south-western to north-eastern gradient in this veld type corresponding to Acocks' (1953) direction of Karoo invasion. However, these two pools are relatively closely related (Figure 1). Acocks (1953) did not recognise any variations in this veld type. However, in his revision (1979) he recognised two main variations, south (36.1) and north (36.2) of the Orange River. The relatively large number of major and residual pools in this veld type (the largest of any of the veld types analysed) may not relate just to large extent of area and transitions but possibly also to the flux resulting from invasion by arid adapted species northwards (Acocks 1953). However, this supposed invasion has not been corroborated (Hoffman and Cowling 1990, Hoffman *et al*. 1999, Hoffman and Ashwell 2001).

Karroid Broken Veld
The analysis of the Karroid Broken Veld shows a major divide between the section of the Great Karoo through to Three Sisters, and patches of this veld type farther to the east. The closely related pools 18 and 17 account uniquely for large areas of the former area and are absent from any of the eastern patches or their surrounds. Karroid Broken Veld east of the Kariega River is mostly represented by the rather heterogeneous pool 20, which also links strongly with

the Central Lower Karoo patches east of the Kariega River. Acocks (1979) completely revised his 1953 version of this veld type and introduced three variations in the Great Karoo. Karroid Broken Veld east of the Kariega River corresponds to his Eastern Variation (26.3c) and is not supported by the analysis as an entity separate from some its neighbours. It is also not closely allied to his generally well-substantiated unit of Karroid Broken Veld in the main section of the Great Karoo (26.3a and 26.3b). His division of the Great Karoo into western and central variations is not substantiated

Veld types of the south-eastern Nama-karoo

The main patch and other patches of Central Lower Karoo west of Aberdeen (Acocks' 1979 Variation (30.1)) are well represented by pool 19 but patches further east (Acocks' 1979 Variation (30.2)) are not or only weakly so. Presence of pool 19 and absence of pools 18 and 17 suggest that the main part of this veld type should have been extended about 20km farther to the west in Karroid Broken Veld. However, given that pools 19, 18 and 17 are very closely related (Figure 1), one could argue that Acocks should have joined the western parts (Variation (30.1)) to Karroid Broken Veld of the Great Karoo, and (based on his sample sites) completely revised the areas to the east together with revision of other veld types and the boundaries in the south eastern Nama-karoo. Pool 20 suggests that he could have fused much of his eastern Central Lower Karoo and eastern Karroid Broken Veld to form a new Central Lower Karoo type. However, pool 20 is very similar to pool 24 (Figure 1), which is a strong link to all the remaining succulent and false veld types in the south-eastern Karoo. The analysis suggests that Low and Rebelo (1996), in their simplification of Acocks' veld types in the Great Karoo, should not have placed their east west divide as far west as Beaufort West. Low and Rebelo's (1996) incorporation of the Steytlerville Karoo into their eastern Karoo unit is partly supported by the analysis.

The Noorsveld veld type as mapped by Acocks is not well supported by the analysis with the most prevalent pool 24 occurring even more extensively in False Karroid Broken Veld. Pool 24 is also the best-represented pool in False Karroid Broken Veld, Spekboomveld and in False Central Karoo in the east and is often located well away from the Noorsveld map unit. With buffering of Spekboomveld, a high proportion of sites of pool 24 is in the general vicinity of Spekboomveld. Acocks (1979) states that 'There is a good deal of overlapping along the boundary (of Noorsveld) with the Spekboomveld and it appears that Noorsveld can replace Spekboomveld through eating-out of the spekboom and spreading of the noorsdoring'.

It appears that the often overwhelming dominance of noors (*Euphorbia coerulescens*) and spekboom (*Portulacaria afra*) species may have tended to bias against recognising substantial floristic similarities between these types and with some other types (see Vlok *et al*. 2003). False Karroid Broken Veld, other than the plains around Cradock, may not have deviated that far from its supposed Spekboomveld-like status as Acocks assumed. It would also appear that the same might apply to much of his False Central Lower Karoo which he regarded as 'transitional to the formally existing belts of woodland and Spekboomveld' (Acocks 1979). His descriptions in both 1953 and 1979 on False Central Lower Karoo are very short and possibly indicate that he regarded it as a 'minor' veld type. Given also the very close relationship between pools 24 and 20, it appears that all his veld types of the south-eastern part of Nama-karoo could have been sunk into a single veld type with the recognition of variations such as Central Lower Karoo and possibly a Cradock plains type transitional to False Central Upper Karoo. However, it is equally possible that a number of his finely mapped units of veld types in the south-eastern Karoo are valid. This may relate to Acocks' sample sizes possibly being too large to allow his data to reflect the relatively fine-scale pattern of veld types mapped in this part of the Eastern Cape.

Karroid Merxmuellera *Mountain Veld Replaced by Karoo*

Sites of the small pool 41 all fall in or very close to the area of the veld type Karroid *Merxmuellera* Mountain Veld Replaced by Karoo mapped on the Nieuweveld Mountains north of Beaufort West. Pool 25 agrees with Acocks' linking of the Nieuweveld Mountains area with the other areas of this veld type mapped to the east. It also agrees with his statement (Acocks 1975) that 'it could well have been shown as occurring around the margin of nearly all the Karroid *Merxmuellera* Mountain Veld'. However, several other pools dilute the identity of this unit, especially in the east. Also in the west, Acocks (1979) revised the extent of his mapped higher altitude grassy Karroid *Merxmuellera* Mountain Veld to form a subdivision of this type on the Nieuweveld Mountains as far west as 'Theekloof' Pass near Fraserburg. It is uncertain how he would have mapped this extension or mapped the consequential changes to the published version of Karroid *Merxmuellera* Mountain Veld Replaced by Karoo.

Conclusions

Acocks did not provide a higher level of organisation of his veld types for the Nama-karoo biome. Our analyses showed that the vegetation of Nama-karoo can be floristically partitioned into a western cluster centred on Arid Karoo and Orange River Broken Veld and a semi-arid part made up of two less clearly distinct clusters. These last two clusters correspond to, firstly a broad belt from the Karroid Broken Veld of the Great Karoo, through Central Upper Karoo to False Central Upper Karoo, and secondly the eastern area of the biome, marginal to thicket and grassland types.

The analysis supports Acocks' (1979) revised concept of Orange River Broken Veld and to a large extent his Arid Karoo and False Central Upper Karoo veld types. A number of his subdivisions of veld types are also substantiated, and he would probably have been justified in raising two of these to veld type status. These are the eastern and western sections of Orange River Broken Veld and the northern Blomkoolgannaveld and the Driedoringveld of the Arid Karoo.

The analysis confirmed that the Central Upper Karoo and False Arid Karoo are nebulous units with gradual transitions to most neighbouring veld types. Boundaries of the types can, therefore, only be very approximate. Although this may serve as some justification of Acocks' (1979) decision to reassign the southern section of Arid Karoo to False Arid Karoo, species pool 13 (Figure 3) suggests he could have maintained the separation.

Not supported by the analysis are the False Succulent Karoo and several veld types, or parts of veld types, in the south-eastern Nama-karoo east of the Kariega River. These are False Central Lower Karoo, False Karroid Broken Veld and eastern fragments of Karroid Broken Veld and Central Lower Karoo. This may relate to Acocks' sample sizes being possibly too large to allow his data to reflect the relatively fine-scale pattern of veld types mapped in this part of the Eastern Cape. The analysis suggests that the karroid vegetation in the broad vicinity of Spekboomveld of the escarpment and its immediate basin tend to group with this veld type at Acocks' sampling scale (see also Vlok *et al*. 2003).

Acocks' notion of 'False' veld types could not be fully evaluated by the present study since the supposed previous condition is reflected in veld types most of which lie outside the Nama-karoo and were not analysed. However, the strong ties indicated by the study between the Central Upper Karoo and the False Arid Karoo corroborates Acocks' (1953) view that the latter veld type was originally derived from Central Upper Karoo. There is still much uncertainty regarding the former conditions of vegetation in the Karoo (Dean *et al.* 1995, Dean and Milton 2003, Meadows 2003).

Acknowledgements — We thank the editors for inviting us to submit this paper for the special issue honouring John Acocks' unparalleled contribution to the understanding of the vegetation of South Africa. We also thank our referees for their useful and constructive comments.

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Edited by MT Hoffman and RM Cowling