



Biomes and Bioregions of Southern Africa

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Figure 3.1 Visual collage of biome diversity.

1. Biomes

1.1 The Biome Concept

The terms biome, ecoregion and bioregion of academic ecology are becoming increasingly used by those concerned with management and conservation of natural resources. These units have broad-scale applicability to those who have to develop conservation and management strategies over large areas. This chapter attempts to re-define the biome classification of the region encompassing South Africa, Lesotho and Swaziland in the context of the new vegetation map in the atlas section of Chapter 18. We also introduce the first consistent classification of 'bioregions'—subordinate units to a biome.

The key to understanding the concept 'biome' is rooted in the issue of scale and in the concept 'biotic community'. The concept 'community' ('biotic community') itself is marred by a history of inconsistent use and interpretation to such an extent that some view it as a nonconcept (Peters 1991). If we define 'community' very broadly as *an assemblage of living organisms sharing the same portion of space during a certain period of time*, then this all-encompassing definition applies to biome as well. The real difference is in scale. Biome is viewed as a high-level hierarchical (hence simplified) unit having a similar vegetation structure exposed to similar macroclimatic patterns, often linked to characteristic levels of disturbance such as grazing and fire. The biome can be considered a kind of 'subcontinental biotic supercommunity'. Cox & Moore (2000) call it a 'large-scale ecosystem'. As a high-level hierarchy unit, biomes are not characterised by individual species (which appropriately characterise units at the more detailed lower hierarchical levels) but mainly by the emergent properties of vegetation structure and associated climate or any other applicable broad-scale environmental factors (O'Neill et al. 1986). Hierarchy theory also suggests that higher-level spatial hierarchy scales (such as biomes) are associated with longer-term time scales although there is a complex interplay between evolutionary (long-term) and ecological (short-term) time scales. Rutherford & Westfall (1986, 1994) provided (at that stage) an exhaustive review of the complexity in defining biomes, also referring to five criteria (maximum global limits, mapping scale limits, primary and secondary bases for classification, and excluded areas) described further below. The main proponents in biome (or an equivalent) definition were either those emphasising the overriding role of climate acting at broad scales (Schimper 1898, 1903, Rübél 1930, Schimper & Von Faber 1935, Weaver & Clements 1938, Holdridge 1947, 1967, Walter 1973, 1976, Whittaker 1975, Walter & Box 1976, Walter & Breckle 1991, Rivas-Martínez 1995, Polis 1999, Krebs 2001) or those using a combination of life forms matching (not always perfectly) the major climatic patterns (Box 1981, 2002, Rutherford & Westfall 1986, 1994, Cox & Moore 2000, Mucina 2000).

The quantitative link between climate and life form combinations serves as basis for construction of biome models making use of key ecophysiological principles (see below). Bond et al. (2003, 2005), Woodward et al. (2004), Bond (2005) and Bond & Keeley (2005) found that the extent of the modern biomes (especially in C_4 -dominated grasslands, savanna as well as in fynbos—all 'fire-driven ecosystems' (FDE) *sensu* Bond et al. 2003) is at variance with classical climate potential models of biomes. These findings strongly suggest that the biome concept has to be revised to recognise the role of large-scale disturbance as an important factor shaping the zonal vegetation.

Strictly speaking the term biome includes both plant and animal communities, as its original American roots (Clements &

Shelford 1939) suggest. Because of the dominant nature of vegetation cover in (nearly) all terrestrial ecosystems, biomes have been based only on vegetation characteristics.

In vegetation ecology, the concept of a plant community on a (sub)continental scale was called a 'formation' (Grisebach 1872, Dansereau 1957, Fosberg 1961, Mueller-Dombois & Ellenberg 1974; see Beard 1978 for a review). Probably because the term 'formation' was later used as part of formal syntaxonomic hierarchies of the American and Russian schools (compare Whittaker 1978 and Aleksandrova 1978) in very different ways, the term has largely been abandoned by the scholastic community or is used in an informal context. Although our 'biomes' are thus structural 'formations' in the original sense of Grisebach (1872), we prefer the former term.

This chapter introduces some of this information but mainly compares our units with those of other previous approaches and also makes certain comparisons (including climatic) across our biomes. This main focus is also applied to our bioregions that lie at a level between the biome and the vegetation types. Details on each biome are given in the respective chapters of this book.

1.2 Biomes of Southern Africa: Major Patterns

Southern Africa boasts a wide range of biomes. The relatively moist, mostly winter-rainfall region, encompassing the Fynbos Biome in the west and its drier climatic counterpart termed the Succulent Karoo Biome, forms the smallest of the world's six floristic kingdoms (Takhtajan 1986, but see Cox 2001), often draped over the Cape Fold Mountains and sandy lowlands of the southwestern Cape. The Succulent Karoo Biome of the Richtersveld, Namaqualand and the Little Karoo has not only the highest diversity of succulent plants in the world, but is the most species-rich semidesert on our planet. The summer-rainfall Savanna Biome of the north and east of the region represents the southern extension of the largest biome of Africa. The summer-rainfall Grassland Biome of the cooler, elevated interior is poorly represented elsewhere in Africa and is home to a wealth of species limited to southern Africa. The unique Indian Ocean Coastal Belt (IOCB) of South Africa with its recurrent extant enclaves of forest represents the southernmost extent of coastal (sub)tropical forests of the wet, tropical and subtropical seaboard of East Africa. The Desert occupies a small extent of our mapping area in the extreme northwest but, importantly, forms the southern tip of the winter-rainfall domain of the Namib Desert as well as a summer-rainfall Gariep Desert with affinities to the central-north parts of the Namib Desert. The Albany Thicket Biome, with a combination of plant forms intermediate between Savanna, Nama-Karoo and Subtropical Forest, represents an unusual structural, floristic and evolutionary ancient type of note in the subcontinent. The mostly summer-rainfall Nama-Karoo Biome is possibly the least species-rich, yet it holds many intriguing relationships with its six directly neighbouring biomes. The Afrotemperate Forests in southern Africa are highly distinctive and are also characterised by their small and patchy occurrence over the wetter parts of the winter- and summer-rainfall areas of the region. They are clearly part of the global warm-temperate forest biome. Most of these patches are too small to be shown in Figure 3.2. The Subantarctic Tundra and Polar Desert Biomes on the Prince Edward Islands in the Southern Indian Ocean are discussed in Chapter 15 and are not referred to further in this chapter.

The two most cited sets of previous works on biomes in southern Africa are Rutherford & Westfall (1986, 1994) and Low & Rebelo (1996, 1998) following on the seminal work of Huntley

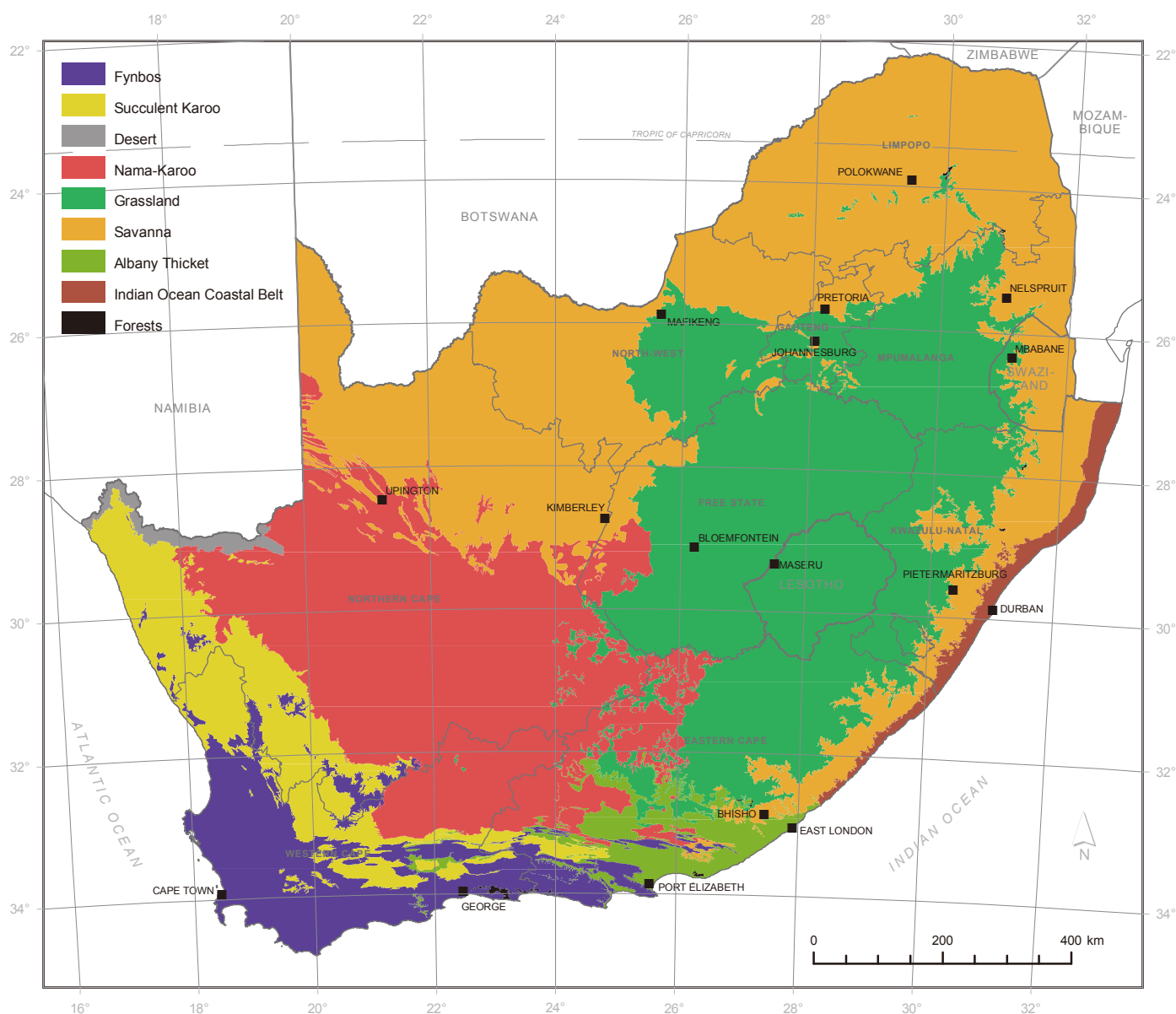


Figure 3.2 Biomes of South Africa, Lesotho and Swaziland.

(1984). The biome concept has been examined in some detail in Rutherford & Westfall (1994) and Rutherford (1997) and applied to southern Africa. In contrast to Low & Rebelo (1996, 1998), the criteria Rutherford & Westfall (1994) applied for a biome were explicit and derived from the globally applicable literature (e.g. Hansen 1962, Odum 1971, Smith 1974, Godman & Payne 1979).

Rutherford & Westfall (1994) emphasised that:

- (1) A biome is the largest land community unit recognised at a continental or subcontinental scale and therefore does not recognise any subsets of a biome as a 'biome of lower rank'.
- (2) Biome patches should be of a viable and minimum size (also to acknowledge the zoological components of a biome) (about 20 km in shortest cross distance).
- (3) Biomes are defined primarily on combinations of dominant life or growth forms and not on the basis of taxonomic characteristics (floristic nor faunal) or nondominant elements.
- (4) Biomes are defined secondarily on the basis of major climatic features that most affect the biota, i.e. not climatic indica-

tors that may happen to correlate with the biome but are ecologically insignificant or irrelevant.

- (5) Biomes do not include unnatural or major anthropogenic systems, although systems irreversibly changed by man (e.g. long-term, severe overgrazing) that are self-sustaining in their present state, are included.

The current work deviates only from the second and third criteria above largely because we are here deliberately biased towards vegetation and its floristic diversity. Only botanical elements are considered (with no consideration of faunal elements nor of their scale requirements—home ranges etc.). The biomes are made up of vegetation units defined on floristic criteria (not purely structural criteria) and no scale limitation was recognised (other than that the vegetation unit should be above the level of plant community). The biomes are partly derived from a bottom-up approach which accounts for the perfect match between biome boundaries and floristically determined boundaries. This should not distract from the broad yet distinctive floristic links with structurally determined biomes as shown by Gibbs Russell (1987), ultimately also by our approach. The biomes are also clearly in keeping with the climatic criteria of biomes and they

correlate with climatic parameters that are biologically meaningful (see below).

The current work recognises two biomes in addition to those of Rutherford & Westfall (1994) and Rutherford (1997). The first is the Albany Thicket Biome which Rutherford & Westfall (1994) referred to as unmappable 'dwarf forest' of the Eastern Cape and included in their Savanna Biome. This biome partly corresponds to the Low & Rebelo's (1996) 'Thicket Biome', but the latter was much more extensive than the Albany Thicket Biome (including much of the Western Strandveld; see Chapter 4 on Fynbos). The second newly distinguished biome is the much transformed IOCB which was mapped as Savanna by Rutherford & Westfall (1994) but, as also pointed out by them (p. 74), was regarded as not fully satisfactory in the area. In this area, the current work retains as Savanna Biome only the inland strip parallel to the IOCB. Given no constraints of scale, the present work also includes many groupings of azonal vegetation units, which are not regarded as part of any biome in zonal terms, but appear as biomes merged into the background on both (scale-limited) biome and bioregion maps. Many biome boundaries are different owing to the different criteria used and to availability of new information, yet many of the boundaries remain nevertheless broadly similar. The greatest relative change (increase) in area of biome compared to that of Rutherford (1997) is in the Desert and Afrotropical Forests. The most northerly and driest parts of the Succulent Karoo Biome of Rutherford (1997) in the vicinity of the lowest reaches of the Orange River are now regarded as part of a winter-rainfall Desert (although it is clear that at least some patches of the Succulent Karoo Biome will be upheld northwards in southwestern Namibia). Degrees of correspondence between the currently recognised biomes and other recent biome classifications are given in Table 3.1.

1.3 Biogeographical Approaches

There have been a number of other large-scale compartmentalisations into natural areas of our mapping area that approximate our biome scale.

White (1983) distinguished five phytocoria (phytogeographical units) in our region based on richness of their endemic floras at the species level. Degrees of correspondence between the biomes and the phytocoria of White (1983) are given in Table 3.2. There is fair correspondence between the Cape

Phytochorion and the Fynbos Biome as well as between the Guineo-Congolian Phytochorion (Usambara-Zululand Domain) and the IOCB. White (1983) recognised most of the more mesic parts of the Grassland Biome as part of his Afrotropical Phytochorion.

Gibbs Russell (1987) clearly showed that floristic links were closer between the Succulent Karoo Biome and the Fynbos Biome than between the Succulent Karoo and the Nama-Karoo Biomes. Linder et al.'s (2005) analysis divided our Savanna Biome into an eastern and northern form on the one hand and a Kalahari form (including western parts of the Central Bushveld Bioregion) on the other.

Siegfried (1989) provided a map of the biomes of our mapping region based on Rutherford & Westfall (1986) and for the savanna areas on Huntley (1984). The savanna areas here and in Huntley (1997) were divided into Arid Savanna and Moist Savanna Biomes. These two functionally important groupings are discussed further in the Savanna Chapter in this book.

Burgess et al. (2004) provided a map of the ecoregions of Africa and some of these units as well as some of their hierarchically higher units relate to our biome level. In this section we examine the relationship between their work and our work at biome level. First, it is important not to confuse our terms and concepts of 'biomes' and 'bioregions' with those used by Burgess et al. (2004). They group their most detailed-level units (ecoregions) into a dual hierarchy. (Discussion of various approaches to 'ecoregions' is found in section 2.2 on Bioregions.) In a biogeographical framework they group ecoregions into 'Bioregions' which in turn are grouped into 'Realms'. Within a 'habitat framework' they group ecoregions into 'Sub-biomes' which in turn are grouped into 'Biomes'. Within our mapping area, they recognise only two 'Bioregions'. Areas corresponding to our Fynbos and Succulent Karoo Biomes fall within a 'bioregion' called 'Cape Floristic Region' while the remaining area is part of a bioregion called 'Eastern and Southern Africa'. In our mapping area their 'bioregion' level, contrary to ours, generally lies above that of our biomes and, indeed, their biomes. It is unfortunate that Burgess et al. (2004) failed to be more explicit about their classification criteria. Their terminology shows a curious mixing of phytogeographical and vegetation-ecological systems.

Burgess et al. (2004) recognised six biomes in our mapping region:

The biome termed 'Mediterranean Forests, Woodlands, and Scrub' comprises their 'Albany Thickets' (sic), 'Lowland Fynbos and Renosterveld' and 'Montane Fynbos and Renosterveld' bioregions (and in South Africa these are not divided into sub-biomes). 'Lowland Fynbos and Renosterveld' and 'Montane Fynbos and Renosterveld' together closely approximate the extent of the Fynbos Biome (82%). There is some agreement regarding the core area of the Albany Thicket Ecoregion and the Albany Thicket Biome, but overall correspondence is only 33% (Table 3.3).

The biome termed 'Deserts and Xeric Shrublands' includes areas corresponding to our Desert, Succulent Karoo and Nama-Karoo Biomes as well as to two of our Savanna Bioregions, namely Eastern Kalahari Bushveld and Kalahari Duneveld. Their biome is not divided into

Table 3.1 Correspondence between recent biome classifications for South Africa, Lesotho and Swaziland and those presented in the current work.

Biome	Overlapping area (%)			
	Rutherford & Westfall (1986)	Low & Rebelo (1996)	Rutherford (1997)	Simplified biome map (Figure 3.2)
Albany Thicket	0	50	0	100
Desert	0	0	8	100
Forests	23	78	23	100
Fynbos	76	81	75	100
Grassland	85	82	85	100
Indian Ocean Coastal Belt	0	0	0	100
Nama-Karoo	94	93	94	100
Savanna	82	88	80	100
Succulent Karoo	75	78	75	100

Table 3.2 Degree of correspondence (%) between the biomes and phytocoria after Linder et al. (2005) and White (1983).

Phytocorion	Biome								
	Albany Thicket	Desert	Forests	Fynbos	Grassland	Indian Ocean Coastal Belt	Nama-Karoo	Savanna	Succulent Karoo
Linder et al. (2005)									
Cape	55		56	77			2		44
Eastern Karoo	21				45		15	24	
Kalahari					5			19	
Karoo Transition							5	4	
Namib-Karoo		100		6	1		77	3	47
Natal	14		29		49	69		46	
Somalian								1	
Zambesian-Central			3					2	
<i>Not classified</i>	10		12	17		31		1	9
White (1983)									
Zambeian			3		2			33	
Cape	10			68			1		11
Karoo-Namib	13	100		25			74	3	89
Afromontane			70	5	17			2	
Kalahari/Highveld	16		5		69		25	43	
Tongaland-Pondoland	61		21	2	12	96	1	19	
<i>Not classified</i>						4			

sub-biomes in South Africa. There is a close correspondence (in South Africa) between their 'Nama Karoo Ecoregion' and the Nama-Karoo Biome (91%) and there is also a reasonably close correspondence between the 'Succulent Karoo Ecoregion' and the Succulent Karoo Biome (77%).

The biome 'Montane Grasslands and Shrublands' corresponds generally to our Grassland Biome, but Burgess et al. (2004) include in their biome their 'Maputaland-Pondoland Bushland and Thickets' Ecoregion, which corresponds closely to our Eastern Valley Bushveld and Thukela Bushveld. With this anomaly excluded, there is an 88% correspondence with the Grassland Biome. They differentiate the high-altitude grassland of the Drakensberg from the rest of the grassland as an 'Alpine Moorland' Sub-biome.

The biome termed 'Tropical and Subtropical Grasslands, Savannas, Shrublands, and Woodlands' corresponds generally to our Savanna Biome (with the notable exception of our Kalahari Bioregions and Zululand Lowveld areas). They differentiate their biome into two sub-biomes, namely 'Acacia Savanna Woodland' and 'Mopane Woodland'.

Their biome called 'Tropical and Subtropical Moist Broadleaf Forests' corresponds approximately to our Afrotropical Forests together with the IOCB. At the sub-biome level they

separated an 'Afromontane Forest' from an 'Eastern African Lowland Forest-grassland Mosaic', the latter corresponding more closely to our IOCB (87%). In South Africa we recognise their 'Mangroves Biome' only as an azonal vegetation type—Mangrove Forest. Within this unit in South Africa, they do not differentiate at sub-biome level.

Using a cluster analysis of plant species distributions from a variety of sources, Linder et al. (2005) derived seven phytocoria within or entering our mapping domain. These are: (1) 'Namib-Karoo' in Namaqualand, most of the Karoo interior and southern Namibia; (2) 'Cape' in the Western and Eastern Cape Provinces and approximating the area of the Fynbos Biome; (3) 'Kalahari' in the northern parts of the Northern Cape Province and western parts of the North-West and Limpopo Provinces and extending through Botswana to cover most of central and northern Namibia; (4) 'Karoo transition' in scattered parts in the north of the Northern Cape and central Botswana; (5) 'Eastern Karoo' over most of the Free State and some adjoining areas in the North-West and Northern and Eastern Cape Provinces; (6) 'Natal' along the eastern seaboard east of the main escarpment from around East London northwards, including nearly all of KwaZulu-Natal and Mpumalanga, all of Gauteng and most of Limpopo Province; and (7) 'Zambeian-central' in the northeastern extremity of South Africa extending north of the Limpopo through the eastern half of Africa to northern Tanzania. Table 3.2 gives the degree of correspondence of these phytocoria with our biome units. There is

good correspondence between the Cape Phytocorion and the Fynbos Biome and fair correspondence between the Eastern Karoo Phytocorion and the less mesic parts of the Grassland Biome. However, the Natal Phytocorion does not distinguish between Savanna, IOCB and the more mesic parts of the Grassland Biome. Similarly, the Namib-Karoo Phytocorion does not distinguish between the Desert, Succulent Karoo and Nama-Karoo Biomes which Linder et al. (2005) suggest may be due to under-sampling and to the coarse resolution of their sampling.

1.4 Biome Modelling

Many other approaches to defining biomes include modelling. Equilibrium models for predicting biome distribution represented the first generation models where biome or biota distribution was assumed to be in equilibrium with climate. Holdridge (1947) was the first to attempt to provide a global classification and distribution of life zones (biomes) based on two climatic parameters. Holdridge's classification (and some other similar schemes, e.g. Whittaker 1975) assumes that biomes act as an amorphous whole—in other words, they are not made up of individual components with different climatic sensitivities. A pioneer and remarkably comprehensive equilibrium model was constructed by Box (1981) who defined close

Table 3.3 Degree of correspondence (%) between the biomes and ecoregions of Burgess et al. (2004). *Full name: Tropical and Subtropical Grasslands, Savannas, Shrublands, and Woodlands.

Biome and Ecoregion according to Burgess et al. (2004)	Biome								
	Albany Thicket	Desert	Forests	Fynbos	Grassland	IOCB	Nama-Karoo	Savanna	Succulent Karoo
Deserts and Xeric Shrublands	16.1	100		12.9	8.3		95.1	39.1	90.2
Kalahari Xeric Savanna					0.7		2.5	37.3	
Nama Karoo	15	76.8		1.9	7.6		91.3	1.8	13.1
Succulent Karoo	1.1	23.2		11			1.3		77.1
Mangroves							5		0
Southern African Mangroves							5		0
Mediterranean Forests, Woodlands, and Scrub	37.8		2.4	84.7	0		0.9	0.1	9.7
Albany Thickets	32.8			2.5	0		0.9	0.1	2.1
Lowland Fynbos and Renosterveld	2.6		0.7	37.2					0
Montane Fynbos and Renosterveld	2.5		1.7	44.9					7.6
Montane Grasslands and Shrublands	35.5		19.1	0.5	89.4	7.7	4	17.6	
Drakensberg Alti-Montane Grasslands and Woodlands					3.3				
Drakensberg Montane Grasslands, Woodlands and Forests	27.8		14.3	0.4	38	2.5	3.7	10.9	
Highveld Grasslands					47		0.3	3.8	
Maputaland-Pondoland Bushland and Thickets	7.8		4.8	0.1	1.1	5.2		2.9	
Tropical and Subtropical Grasslands, Savannas*			13.8		2.1				40.2
Kalahari Acacia-Baikiaea Woodlands									2.5
Southern African Bushveld			6.2		0.9				26.4
Zambezian and Mopane Woodlands			7.6		1.2				11.2
Tropical and Subtropical Moist Broadleaf Forests	10.4		64.2	1.8	0.1	86.8	0		3
Knysna-Amatole Montane Forests	1.3		58.5	1.8	0.1		0		0
KwaZulu-Cape Coastal Forest Mosaic	9		5.7		0	59.4			1.2
Maputaland Coastal Forest Mosaic						27.4			1.8

to 100 different plant types and the climatic tolerance ranges of each in terms of an array of climatic variables. He used these to map the combinations of these types globally with reasonable success at the macroscale. A similar, but more practically simplified 'functional group' approach was more formally applied in the BIOME foundation model (Prentice et al. 1992), in which 13 functional groups of plants were defined and related to four major bioclimatic controls. The results for the area of South Africa partly matched some of the biomes, but were at variance with a number of others. Subsequent models included coupled models which derive vegetation type (and structure) and biogeochemical fluxes. Examples include BIOME3 (Haxeltine & Prentice 1996) incorporating various physiological and ecosystem processes (see Hallgren & Pitman 2000 for a critical evaluation). This model has evolved into BIOME4, which attempts to cover the diversity of biome types better (Cramer 2002). Choice of climatic variables is crucial. Leemans (1997) observed that the more superior global vegetation models all included a realistic water balance and/or seasonality. Despite the application of many forms of a priori-defined functional types above, defining functional types remains a 'major problem' and 'experiments or natural perturbations may be the only approach which can differentiate functional types; structure may not be a reliable key' (Woodward & Cramer 1996).

Interest in biome models as mentioned above comes to a large extent from the need to estimate likely changes in carbon stores in the terrestrial biosphere, as a consequence of atmospheric carbon dioxide increase and the associated changing climate (Cramer 2002). In other words, there is likely to be less interest in the precision of boundaries of biomes and the identity of small but floristically important biomes such as the Succulent Karoo. It has also been recognised in some global models that shrubland biomes are more difficult to predict (Woodward et al. 2004).

Clustering climatic ranges of plant taxa have been used to produce 'Bioclimatic Affinity Groups' (Laurent et al. 2004), resulting in the co-occurrence of several such units in the same area. But such multiranging units were not synthesised into units of vegetation assembly.

Biomes and other categories have limitations depending on purpose. 'Categories such as that of ecoregions tend to become self-fulfilling prophecies when experimental designs assume their validity instead of testing their usefulness' (Magnusson 2004). Also, the longer-term identities of biome units have to be questioned where there is ample evidence that biomes in the past have not moved as a whole in response to climate change (Huntley 1991) and most models of the effects of future climate

change expect species to respond independently of their currently associated species, e.g. see Iversen et al. (2004).

1.5 How the Biomes Compare

More detailed descriptions and considerations of each biome are given in the introductory sections of each biome chapter. Here we concentrate on comparisons across biomes.

The biomes are highly disparate in size. Relative areas of the biomes are given in Figure 3.3. There are three large biomes, namely Savanna, Grassland and Nama-Karoo, together accounting for almost 80% of the total area, while Desert and Afrotemperate Forest together account for less than 1% of the area.

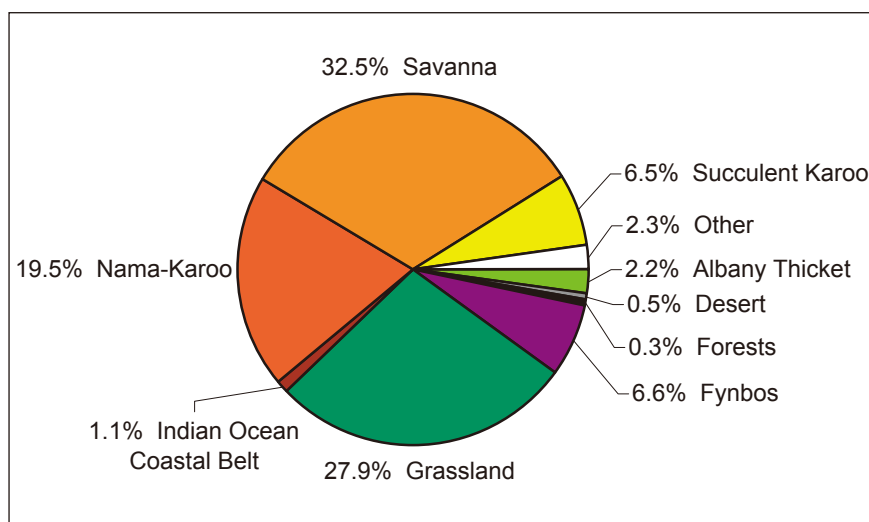


Figure 3.3 Relative proportions of areas of the biomes.

Albany Thicket has the greatest diversity of biome neighbours and borders on seven other biomes (Figure 3.4). This, together with the highly dissected nature and considerable length (> 15 000 km) of the perimeter, allows for possibly high species diversity collectively along this ecotone. Desert borders on the fewest biomes within South Africa (Succulent Karoo and Nama-Karoo), which is what would be expected from the most climatically extreme biome. Just over 40% of potential contacts between biomes in the simplified map (see Chapter 2) do not occur in the region (Figure 3.4). Thus there is little potential exchange of flora between, for example, the Grassland and Succulent Karoo Biomes. Only three of the biomes (Nama-Karoo, Grassland and very marginally Savanna) do not border on an ocean (or at a larger scale on the vegetation of the coastal strips; Chapter 14). Despite Afrotemperate Forest accounting for the smallest biome area of only 0.3% (Figure 3.3), it has the third longest boundary with biomes in the region (Figure 3.4), illustrating its highly fragmented state. More than two thirds of the land boundary of the Succulent Karoo is shared with Fynbos. Much of this interface is highly irregular, thus possibly promoting some floristic intermingling between these two biomes over time (see also below on sharing of taxa). More than half the boundary of Desert borders on Succulent Karoo (in South Africa), while almost half of that of Savanna borders on Grassland.

Boundaries between biomes vary from sharp to very gradual. Examples of sharp boundaries between biomes include those sometimes over only tens of metres between Fynbos on parts of the Cape Fold Mountains and the Succulent Karoo at lower altitude. More intermediate boundaries of a few kilometres wide are often found between the Succulent Karoo and Nama-Karoo Biomes. Very gradual transitions of tens of kilometres can be found, e.g. in some parts of the southern Kalahari between the Nama-Karoo and Savanna Biomes. In a few isolated cases, membership of a biome is equivocal, for example, for some vegetation types at the interface between the Sub-Escarpment Savanna and Sub-Escarpment Grassland of KwaZulu-Natal.

Most of the biome units of this study are incomplete and continue north of the political boundaries of this work. These are: Desert, Afrotemperate Forest, Grassland, IOCB, Nama-Karoo, Savanna and Succulent Karoo. Only Albany Thicket and Fynbos are fully circumscribed within our geographical area. Savanna has by far the longest border with other unmapped savanna to the north of our region (Figure 3.4).

The number of vegetation units per biome varies widely (Figure 3.5a) and is roughly in proportion to the floristic diversity of the biome. Hence the Fynbos Biome with the highest number of vegetation units (119) also has the highest number of species and a high proportion of endemic species (Gibbs Russell 1987). The Nama-Karoo Biome with only 14 vegetation units is also generally species-poor in comparison to other biomes. The IOCB may appear to be somewhat under-represented in terms of number of vegetation types currently recognised, yet on a unit area basis at 0.5 vegetation units per 1 000 km², it is intermediate between Savanna and Albany Thicket (Figure 3.5b). Although the diversity and the number of vegetation types in the Desert Biome is probably boosted by almost 90% of its types bordering directly on the relatively species-rich Succulent Karoo Biome, the relatively high number of types in the biome may also reflect a treatment at a greater level of detail. At the same time, the somewhat lower number of vegetation types per unit area in the Fynbos Biome probably reflects the significant under-sampling in the biome. The mean area of vegetation types per biome is by far the greatest in Nama-Karoo and smallest for Afrotemperate Forest (Figure 3.5c). The vegetation types in Desert and Fynbos are only marginally larger than those in Afrotemperate Forests, again emphasising the high species diversity and its level of geographical clustering in Fynbos (see above regarding detail in Desert).

Gibbs Russell's (1987) analysis of the species (and infraspecific taxa) richness of those biomes compatible with those of this book (and omitting biomes that were included in her analysis north of our mapping area) showed the Fynbos Biome to be the most rich with 7 316 taxa (currently with biome edges including almost 9 000 taxa) and about 52% of this amount in Grassland Biome and 29% in the Succulent Karoo Biome. About 67% of Fynbos Biome taxa, 28% of Grassland Biome taxa and 29% of Succulent Karoo Biome taxa were endemic. There was greatest sharing of taxa between the Succulent Karoo and Fynbos Biomes and least sharing of taxa between the Grassland and Succulent Karoo Biomes. Across South Africa, it has been found that numbers of alien and invasive species are significantly correlated with indigenous plant species richness (Richardson et al. 2005).

Using the biomes as defined in this book (but also extended to cover Namibia and Botswana), Chesselet et al. (2003) analysed the distribution of the 1 663 species of Mesembryanthemaceae, one of the most important families in our region. For the biomes compatible with our mapping area, by far the most species (871)

Biome	Albany Thicket	Desert	Forests	Fynbos	Grassland	Indian Ocean Coastal Belt	Nama-Karoo	Savanna	Succulent Karoo
Desert	■								
Forests	649	■							
Fynbos	5 814	■	2 459						
Grassland	2 519	■	9 765	■					
Indian Ocean Coastal Belt	1	■	■*	■	■				
Nama-Karoo	2 993	361	■	448	9 600	■			
Savanna	2 070	■	7 045	273	18 807	3 737	6 560		
Succulent Karoo	1 555	513	■	8 949	■	■	2 354	■	
Northern border		507	25			27	239	3 004	
Ocean	403	12	76	1 442		879		3	455

Figure 3.4 Lengths (km) of shared boundaries between biomes. Black squares indicate no contact between biomes. *Forest patches touching or surrounded by Indian Ocean Coastal Belt were subsumed into the Indian Ocean Coastal Belt.

occur in the Succulent Karoo, a large number (382) in the Fynbos Biome with lower numbers in the Albany Thicket and Grassland Biomes. The IOCB harbours very few (8), but together with the other above-mentioned four biomes each has 75% or more (up to 93% for Fynbos Biome) endemic to the respective biome.

Comparisons of aspects relating to conservation status of biomes are found in Chapter 16.

1.6 Climatic Relations of Biomes

The general climate of each biome (i.e. averaged over the entire area of the biome and, therefore, representing only a central tendency for a biome) is summarised in the climate diagrams in Figure 3.6. Afrotropical Forests and the area of IOCB experience the highest rainfall. The western parts of the Fynbos Biome and, in the drier areas, the Succulent Karoo Biome have a generally winter-rainfall regime. The Nama-Karoo experiences relatively low levels of rainfall that are concentrated in late summer and early autumn. The Grassland Biome is climatically similar to Savanna but with lower temperatures. The Albany Thicket has a greater and more pronounced bimodal (summer-autumn) rainfall than the Nama-Karoo. The coefficient of variation in

annual precipitation is the lowest in the IOCB and the highest in the arid biomes such as the Succulent Karoo and Nama-Karoo Biomes. The number of frost days per year varies from zero in the IOCB to a maximum in the Grassland Biome. The mean annual potential evaporation is the lowest for the IOCB, with high values in the Nama-Karoo, Succulent Karoo and Savanna Biomes. Note how the IOCB occupies the lower extreme (i.e. moderate) for a number of key climatic variables.

Decision Trees have been used to classify biomes at continental scales (Lotsch 1999). Ellery et al. (1991) used a Decision Tree to present the biomes of Rutherford & Westfall (1986) climatically. Similarly, we derived a more specific and diagnostic climatic explanation of the current biomes from a Classification and Regression Tree using the CART method in S-Plus (univariate splits; Clark & Pregibon 1993 and discussion in Hargrove & Hoffman 2005; Figure 3.7). A simpler, more parsimonious, climatic explanation of the biomes was derived using a Hand Constructed Linear Decision Tree (see Murthy 1998) with multivariate splits but with slightly lower overall predictive accuracy (Figure 3.9). The climatic parameters used were deemed biologically meaningful and were: Mean minimum temperature of the coldest month (Tmin), heat units (HtUnt), annual mean evapo-

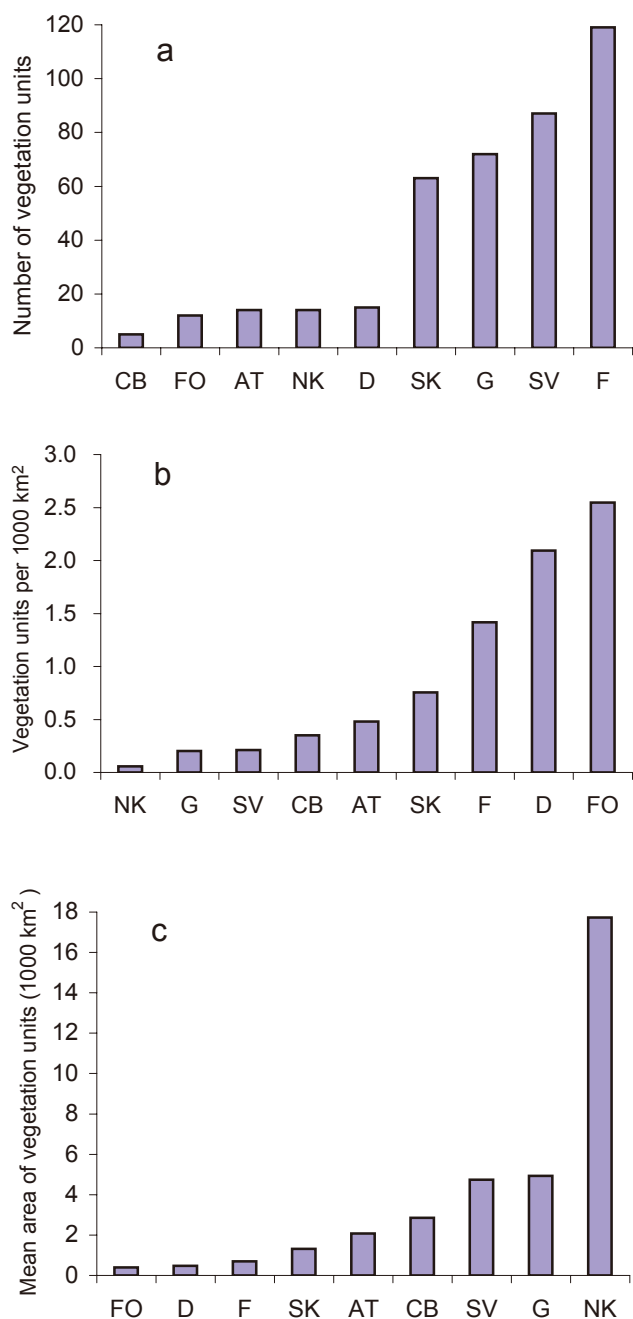


Figure 3.5 (a) Number of vegetation units per biome; (b) mean number of vegetation types per unit area within each biome; (c) mean area of vegetation units per biome. AT Albany Thicket, CB Indian Ocean Coastal Belt, D Desert, F Fynbos, FO Afrotropical Forests, G Grassland, NK Nama-Karoo, SK Succulent Karoo, SV Savanna.

ration (Evap) and soil moisture days in winter (SMDW) and in summer (SMDS). Forests were not included in these analyses owing to their highly fragmented and widely dispersed nature.

Using the more parsimonious and, therefore, more coherent climatic description, IOCB is found mostly under conditions where soil moisture days are high in summer and relatively high in winter. Desert occurs mainly where soil moisture days both in summer and winter are low and evaporation is high. The Grassland climate differs from that of the IOCB by having a lower number of soil moisture days in winter (becoming lower with greater number of heat units) as well as a lower minimum temperature (dropping with increasing evaporation). Savanna climate differs from that of Grassland mainly in having higher

minimum temperatures (level depending on evaporation) and a lower number of soil moisture days in winter (especially in areas of lower annual rainfall). Albany Thicket generally has a moderate number of soil moisture days in summer with moderate levels of evaporation as well as high minimum temperatures (declining with decreasing soil moisture days in winter). Fynbos and Succulent Karoo share some of the climatic attributes of Albany Thicket but differ from it in having lower minimum temperatures (and increasing with number of soil moisture days in winter). Fynbos has a greater number of soil moisture days in winter combined with a fewer number of heat units than in Succulent Karoo. The climatic derivation of Nama-Karoo is in two parts. The southwestern part of the Nama-Karoo has a relatively low number of soil moisture days in summer and moderate minimum temperatures. The northeastern part of the Nama-Karoo shares some of the climatic attributes of Savanna but differs from it in having lower minimum temperatures (declining in areas with higher evaporation).

CART performed between 0.2 and 9.8 percentage points better than the Hand Constructed Linear Decision Tree for seven of the biomes (Table 3.4). However, it was 16.2 and 17.1 percentage points worse for the Desert and IOCB, respectively. The linear extent of these two units was better reflected by the Hand Constructed Linear Decision Tree. Least adequately described climatically by both methods was the Albany Thicket Biome with less than 66% of its area predicted correctly. The biomes as mapped by CART are given in Figure 3.8 which also shows which areas (almost always on the margins) were incorrectly mapped. The correctly predicted areas from climate, therefore, reflect almost all of the core areas of the biomes and most of the error is limited to the transitional areas between biomes.

Climatic relations with biomes are rarely tested experimentally. In a limited study by Agenbach et al. (2004a), using reciprocal transplants of species across a boundary between the Fynbos and Succulent Karoo Biomes, it appeared that at least some Fynbos species were environmentally (including soils) limited, whereas at least some Karoo species may be limited in their distribution by fire and biotic interactions and not by their environment at this biome interface. It is thus clearly demonstrated, from local studies, that climate is not the sole determinant of vegetation distribution (Agenbach et al. 2004b). There may be boundaries between other biomes in the region which are not (only) determined by climate. The interface between our Savanna and Grassland Biomes may be one such possibility (Bond et al. 2003, 2005).

Threats of climatic change on a biome scale are usually discussed within each biome chapter, at least in terms of change in temperature and water availability. Possible effects of future levels of solar ultraviolet-B radiation on plants in South Africa are discussed by Musil et al. (1999). Those areas of South Africa with the highest current levels of UV-B radiation (Gariep Desert, Bushmanland and Kalahari Duneveld) should remain so but at even higher levels at around the middle of the 21st century.

1.7 Southern African Biomes in Context of Walter's Scheme

There are several global biome schemes available (see above for ample references), but an alternative one deserves particular attention not only because of its detail of elaboration (the actual map is accompanied by a series of monographs featuring the biome patterns in the light of ecophysiology and community ecology), but also due to its conceptual handling of zonality, intrazonality and azonality—one of the leading principles of the classification philosophy underlying our Map. It is the system

of zonobiomes of Heinrich Walter (Walter 1962, 1968, 1973, 1976, Walter & Box 1976, Walter & Breckle 1991, etc.).

Walter (for references see above) subdivided the terrestrial surface of the earth into nine zonobiomes, underpinned by the zonal character of climate (Table 3.5). Recognising the occurrence of broad transitions between these units, he further introduced the concept of zono-ecotones, calling them 'tension zones between two zonobiomes in which one vegetation type is being replaced by another...' (Walter & Box 1976).

According to the insert map in Walter & Box (1976) the territories of South Africa, Lesotho and Swaziland fall within four zonobiomes (II, III, IV and V) and two zono-ecotones (IV-III and III-II). The only direct match between our biome system and that of Walter is the identity of the Fynbos Biome and the zonobiome IV. Walter & Box (1976) classified the Fynbos Biome (explicitly) as one of the sub-zonobiomes of the global mediterranean biome (sometimes also called 'ethesial biome'). Our Succulent Karoo corresponds to zono-ecotone IV-III and partly to the zonobiome III, most probably through the 'sub-zonobiome with winter-rainfall' according to Walter & Box (1976). Walter's zonobiome III in southern Africa further covers the Desert Biome and western and central parts of the Nama-Karoo Biome. The eastern Nama-Karoo and Kalahari are classi-

fied by Walter as zono-ecotone III-II. The mapped extent of the zonobiome V in southern Africa is too generous as it comprises most of the southern Cape, Albany Thicket and the IOCB. The last-named should be best served as part of the zonobiome I (generally underestimated on the East African coast by Walter's classification), and the Albany Thicket as part of zono-ecotone I-III (as done for parts of Kenya/Somalia or Venezuela/Colombia). An interesting rare contact between two zonobiomes can be observed along the South Coast—meeting of the zonobiome IV (mainly linked to western oceanic coasts) with the zonobiome V (mainly linked to eastern oceanic coasts), forming a mosaic of the zono-ecotone V-IV (see also Walter & Box 1976). The extent of the zonobiome II (seasonal tropics), as mapped by Walter in southern Africa to encompass all of our Savanna Biome (except for Kalahari) and the Highveld plateau and the Drakensberg Mountain ranges, is also in need of modification—the primary temperate grasslands of our Grassland Biome should rather be re-classified as zono-ecotone II-VII or perhaps zonobiome VII (in the same way as the South American pampas).

2. Bioregions

A bioregion is a composite spatial terrestrial unit defined on the basis of similar biotic and physical features and processes at the regional scale. In this work, the intermediate level of vegetation organisation between that of vegetation type and biome, is the bioregion level.

The term 'bioregion' has been used less frequently than ecoregion (see below) and in very different ways, also globally. In South Africa, Rowe-Rowe & Taylor (1996) used the term bioregion for nine regions in KwaZulu-Natal, seven based on the original bioclimatic regions of Phillips (1973), with the remaining two bioregions deduced from Acocks (1975) and Camp (1995). The resultant units are generally at a level between our vegetation units and our bioregions for the province. The bioregions of Rowe-Rowe & Taylor (1996) have also been used by others (e.g. Avery et al. 2002). In a very different sense, Laurie & Silander (2002) use the term bioregion to equate to the large Cape Floristic Region. In Australia, the term bioregion has been used with the next more detailed level termed 'sub-bioregion' (Pullar et al. 2004) which, judging by the scale of these 'sub-bioregion' units, may approximate the level of our vegetation units. As has been pointed out in Section 1.3, the 'bioregions' of Burgess et al. (2004) are used at a hierarchical level even higher than that of our biomes. We do not refer further to their 'bioregions' here. It is clear that the term 'bioregion' has been used very loosely in the past. We hope that the current treatment will go some way to stabilising the usage of the term and concept.

Although our bioregions (Figure 3.10) represent a level intermediate between biome and vegetation unit, the IOCB is not divided into bioregions within South Africa but can be regarded as approxi-

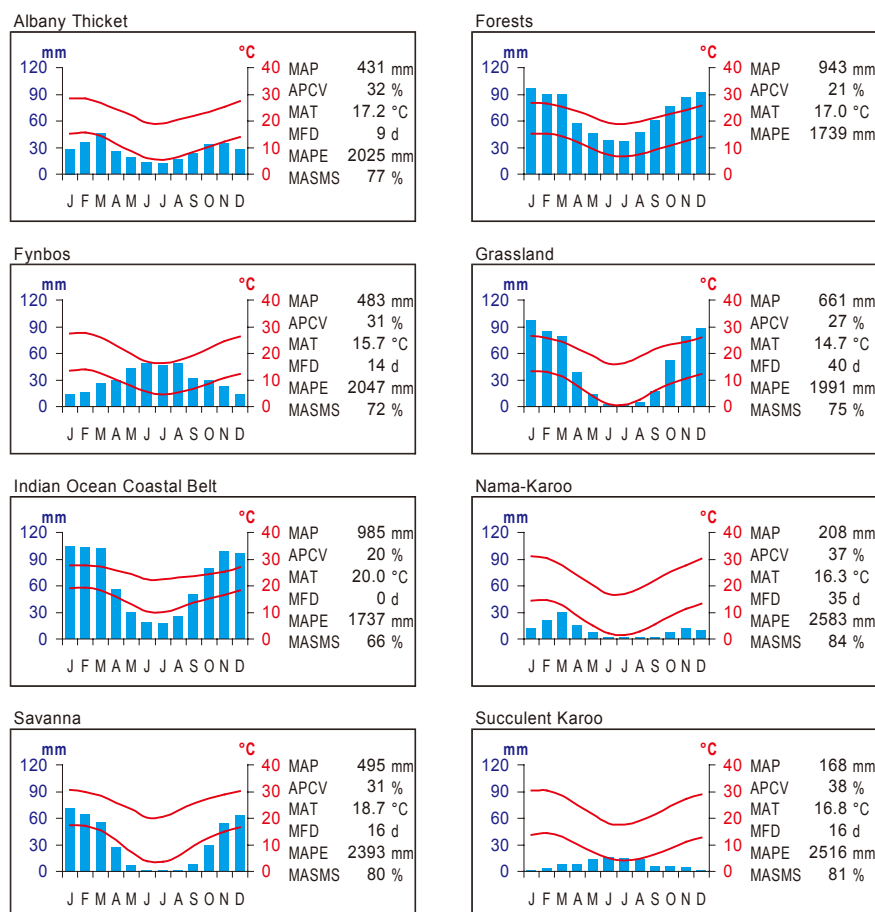


Figure 3.6 Climate diagrams of biomes excluding Desert. Blue bars show the median monthly precipitation. The upper and lower red lines show the mean daily maximum and minimum temperature, respectively. MAP: Mean Annual Precipitation; APCV: Annual Precipitation Coefficient of Variation; MAT: Mean Annual Temperature; MFD: Mean Frost Days (days when screen temperature was below 0°C); MAPE: Mean Annual Potential Evaporation; MASMS: Mean Annual Soil Moisture Stress (% of days when evaporative demand was more than double the soil moisture supply). Note that the diagram for Forests represents the average of a wide range of rainfall seasonality.

Table 3.5 The scheme of Walter’s zonobiomes (after Walter 1976, Walter & Box 1976, Walter & Breckle 1991, Box 2002). Simplified names for the zonobiomes were introduced.

Zono-biome	Name	Characteristics	Zonal Vegetation
I	Equatorial	<ul style="list-style-type: none"> ▪ diurnal climate (mean of daily temperature amplitudes is bigger than the difference between the means for temperatures of the warmest and coldest months) ▪ rainfall usually high (above 100 mm per month), mainly aequinoctiale maxima ▪ zone between approx. 10° N and 5–10° S 	<ul style="list-style-type: none"> ▪ Tropical rain forest
II	Tropical	<ul style="list-style-type: none"> ▪ clear colder and warmer period ▪ strong summer rainfall and extreme drought during colder period of the year (the drought period becomes longer and precipitation lower with increase of distance from the equator); fire-prone 	<ul style="list-style-type: none"> ▪ Tropical and subtropical savannas ▪ Seasonal tropical forests
III	Arid-Subtropical	<ul style="list-style-type: none"> ▪ desert climate: very low precipitation—usually below 200 mm, in extreme desert below 50 mm; high insolation and light reflection; extreme daily temperature amplitude 	<ul style="list-style-type: none"> ▪ Deserts ▪ Semidesert shrublands
IV	Mediterranean	<ul style="list-style-type: none"> ▪ winter rain and summer drought; usually on west oceanic coasts, between 35° and 40° in both hemispheres; fire-prone 	<ul style="list-style-type: none"> ▪ Evergreen microphyllous shrublands ▪ Seasonal evergreen forests ▪ Evergreen broad-leaved forests
V	Warm-Temperate	<ul style="list-style-type: none"> ▪ without pronounced cold winter period; ample year-round precipitation, especially high in summer; usually maritime climate due to prevailing location on eastern seaboard 	
VI	Typical Temperate	<ul style="list-style-type: none"> ▪ short cold (often with snow) period in winter (often lacking in oceanic regions) and warm summers; sufficient cyclonal precipitation 	<ul style="list-style-type: none"> ▪ Deciduous broad-leaved forests
VII	Arid-Temperate	<ul style="list-style-type: none"> ▪ Extreme temperature differences between summer and winter due to continental position; usually low precipitation (bordering on desert climate); some ecosystems fire-prone 	<ul style="list-style-type: none"> ▪ Climatic grasslands (steppe, prairie, pampas) ▪ High-altitude semidesert shrublands
VIII	Cold-Temperate	<ul style="list-style-type: none"> ▪ Cool and wet summers and very cold winters lasting sometimes more than half of the year; absent in southern hemisphere; fire-prone 	<ul style="list-style-type: none"> ▪ Boreal conifer forests (taiga)
IX	Arctic-Antarctic	<ul style="list-style-type: none"> ▪ Cold and wet summers and extremely cold winters; evenly distributed precipitation over year; very short vegetation season 	<ul style="list-style-type: none"> ▪ Dwarf arctic shrublands (tundra) ▪ Polar deserts

mating a bioregion of the much larger belt that extends northwards into East Africa. The Albany Thicket Biome is not easily divided into bioregions and in effect has some properties that agree with those of the bioregion level. These two areas have,

therefore, been included in some of the comparisons below. Afrotemperate Forests were not included owing to their highly fragmented and widely dispersed nature relative to the scale of the bioregion.

Table 3.4 Proportion of each biome correctly predicted (%) by the climatic models using a Hand Constructed Linear Decision Tree (HCLDT) with multivariate splits and a Classification and Regression Tree using the CART method in S-Plus (univariate splits).

Biome	HCLDT	CART
Albany Thicket	63.2	65.1
Desert	86.6	70.4
Fynbos	70.4	80.2
Grassland	77.0	85.1
Indian Ocean Coastal Belt	91.8	74.7
Nama-Karoo	85.6	85.8
Savanna	79.9	86.7
Succulent Karoo	66.7	74.8

2.1 Bioregional Correspondence

There is generally a very poor correspondence of the 16 ‘subdivisions of biomes’ of Westfall & Van Staden (1996) with our bioregions. They simply used mean annual precipitation to subdivide the biomes of Rutherford & Westfall (1994). Our bioregions also differ in many respects from the phytochorial subdivisions of southern Africa where the highest level phytochorion is subdivided first into regions and more finely into domains (Werger 1978).

The *bioregion* also differs from the *ecoregion*. However, since the term *ecoregion* was coined in 1967 (Omernik 1987), it has been used very differently by different sources, complicating the comparisons. Ecoregions, through their availability, have been widely applied for a diversity of purposes (e.g. for units for which plant species diversity could be determined; Kier et al. 2005). Ecoregions have also been used to spawn new units such as combining them with Plant Hardiness Zones to form Plant Adaptation Regions (Vogel et al. 2005).

Ecoregions have often been defined on the basis of a dissection of physical environmental space, i.e. the *ecoregion* boundaries

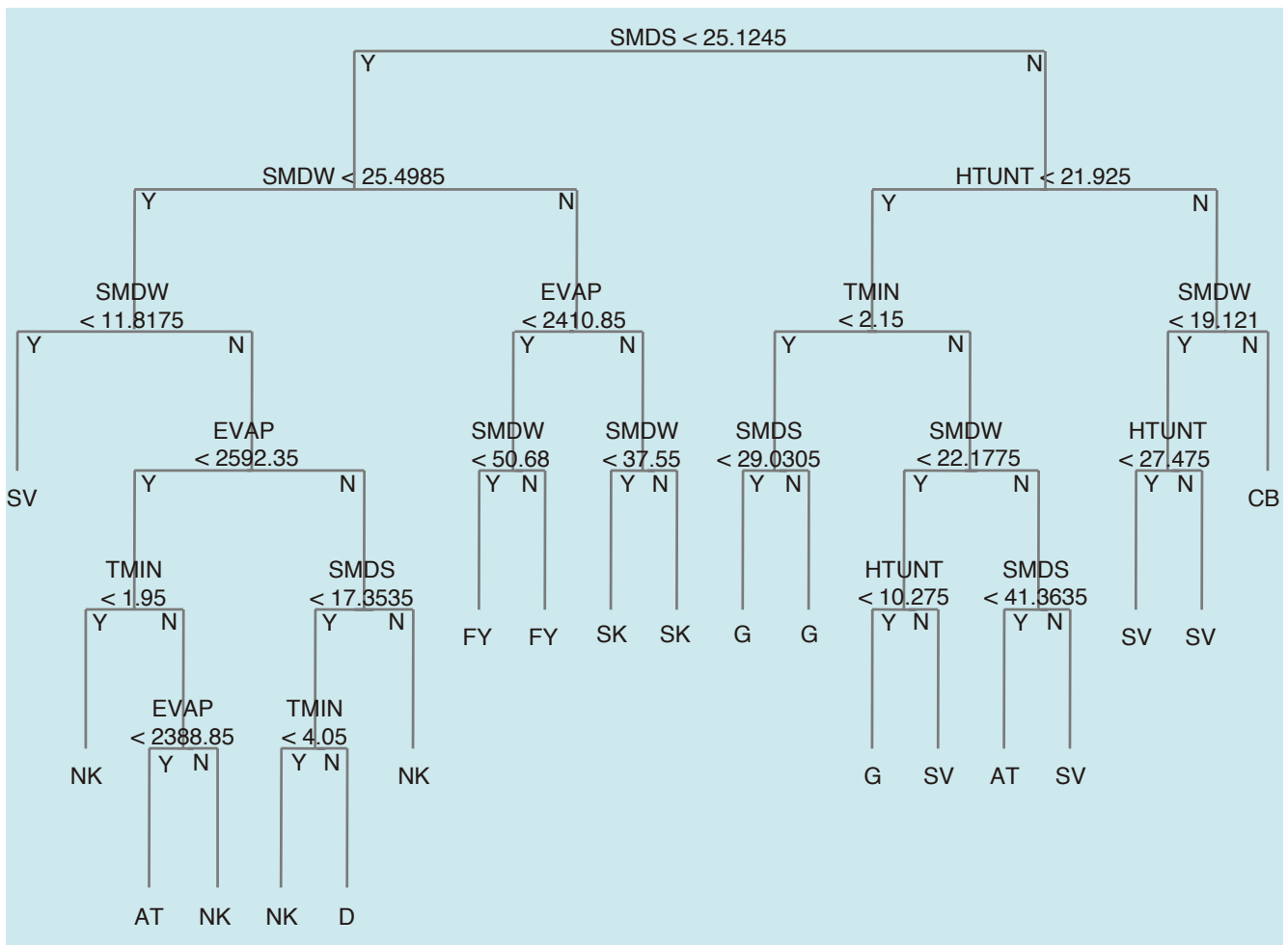


Figure 3.7 Computer printout of the climatic explanation of the biomes from a program for a Classification and Regression Tree using the CART method in S-Plus. TMIN: mean minimum temperature of the coldest month; HTUNT: heat units; EVAP: annual mean (potential) evaporation; SMDW: soil moisture days in winter; SMDS: soil moisture days in summer. AT Albany Thicket, CB Indian Ocean Coastal Belt, D Desert, FY Fynbos, G Grassland, NK Nama-Karoo, SK Succulent Karoo, SV Savanna. Y meets condition, N does not meet condition.

are primarily determined by climate (which 'solves the problem with using other components that are subject to rapid change, such as biota'—Bailey 2004). Ecoregions are sometimes also used at multiple hierarchical levels—e.g. in Australia (Pullar et al. 2004) and in the USA with four levels of ecoregion from the broadest level (Level I) to detailed Level IV (Omernik 2004).

More coherent and biotically inclusive are the ecoregions of Olson et al. (2001) although even within this same lineage, the ecoregions have changed over time (e.g. from Olson & Dinerstein 1998 to Burgess et al. 2004). They have nevertheless attracted a strong following. They have also attracted some criticism e.g. as they have been applied in Indonesia (Jepson & Whittaker 2002).

Our concept of *bioregion* and that of *ecoregion* of Olson et al. (2001) are similar. Both stress that biota are centrally important including distinct assemblages of species. Both are pragmatic units for practical application of conservation and other measures.

However, our bioregions differ from these ecoregions within our mapping area in (1) mapping scale with more detailed units, (2) underpinning by another layer of more detailed sets of biotic assemblages, (3) greater consolidation and coherency of associated climate (in some cases), (4) possible bias toward vegetation and, (5) we believe, more consistent geographical application of the concept. These differences are elaborated below.

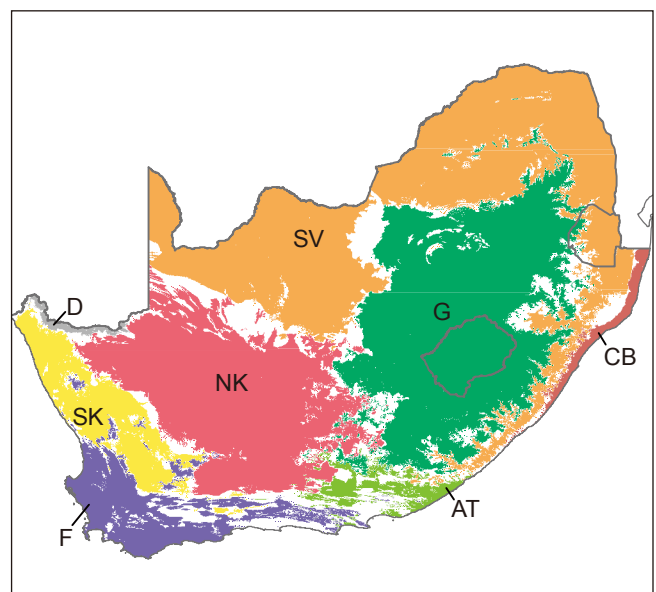


Figure 3.8 Map of the biomes as predicted by the Classification and Regression Tree using the CART method in S-Plus. Areas in white within our domain represent areas of error. AT Albany Thicket, CB Indian Ocean Coastal Belt, D Desert, F Fynbos, G Grassland, NK Nama-Karoo, SK Succulent Karoo, SV Savanna.

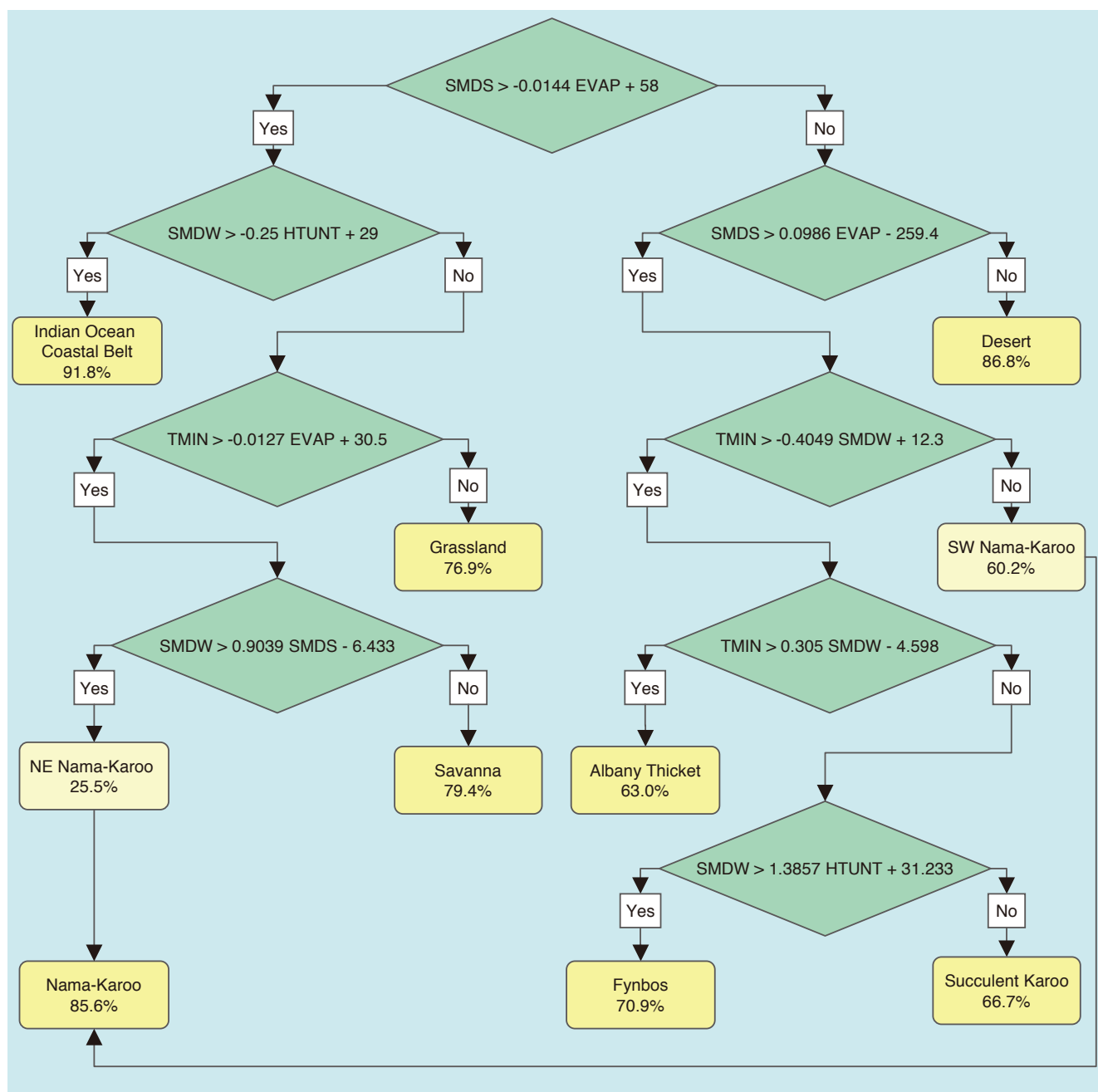


Figure 3.9 Climatic explanation of the biomes using a Hand Constructed Linear Decision Tree. TMIN: mean minimum temperature of the coldest month; HTUNT: heat units; EVAP: annual mean (potential) evaporation; SMDW: soil moisture days in winter; SMDS: soil moisture days in summer. Percentages are the proportion of the biome that was correctly predicted by the decision tree.

The average size of Olson et al.'s (2001) ecoregions globally is about 150 000 km² but is about 102 000 km² within our mapping area. Our bioregions are more finely divided with an average area of 54 000 km², i.e. roughly twice as detailed compared to the ecoregions.

In contrast to the ecoregions, the bioregions are underpinned by another level of biotic detail, namely vegetation types that make up each bioregion. There are on average over 10 vegetation types per bioregion, with the vegetation types (excluding azonal types) averaging just 3 100 km² in area.

Our bioregions follow a principle of regional consolidation, which recognises that a region should not consist of a widely dispersed array of areas and should rather be or tend towards being conterminous. In this sense it is similar in practice to one of the requirements for an ecoregion of Bailey (2004), namely to

circumscribe contiguous areas. At the same time this was fitted to a coherent climatic profile for each bioregion. In this way we try to avoid recognising, for example, a 'Montane fynbos and renosterveld' Ecoregion (Burgess et al. 2004) which stretches as linear discontinuous bands from near Port Elizabeth in the east via the Cape Peninsula and the Roggeveld Escarpment to the Kamiesberg area in Namaqualand, and covers a wide range of climate. Climate tends to be more uniform within the more consolidated areas. Our principle of spatial consolidation for a bioregion also accepts that, despite distinct floristic differences between vegetation types in a bioregion, there are often also numerous species shared between adjacent vegetation types in a region.

Bioregions are focussed on plant diversity, i.e. on the floristic composition of their component vegetation types (and presum-

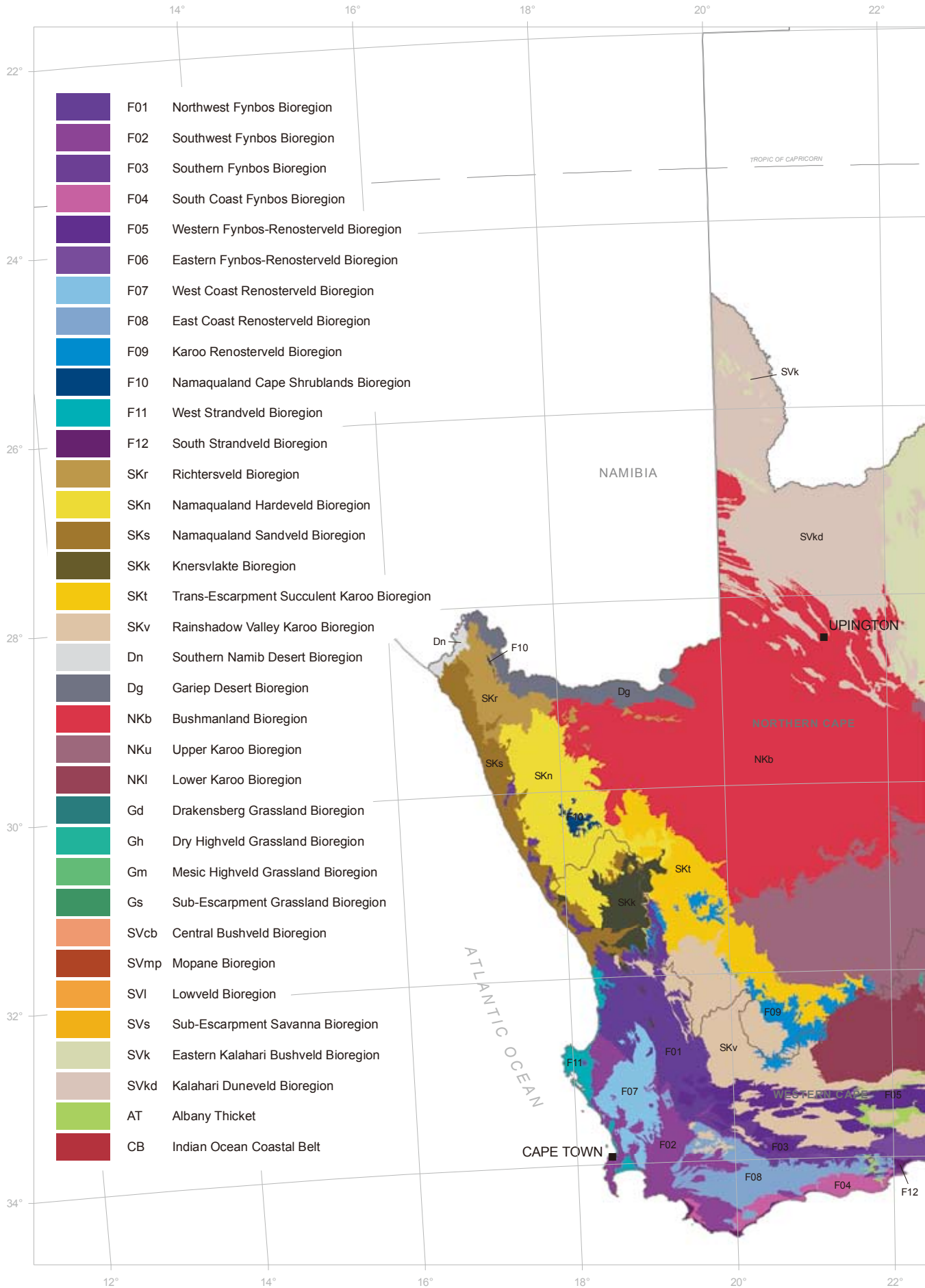
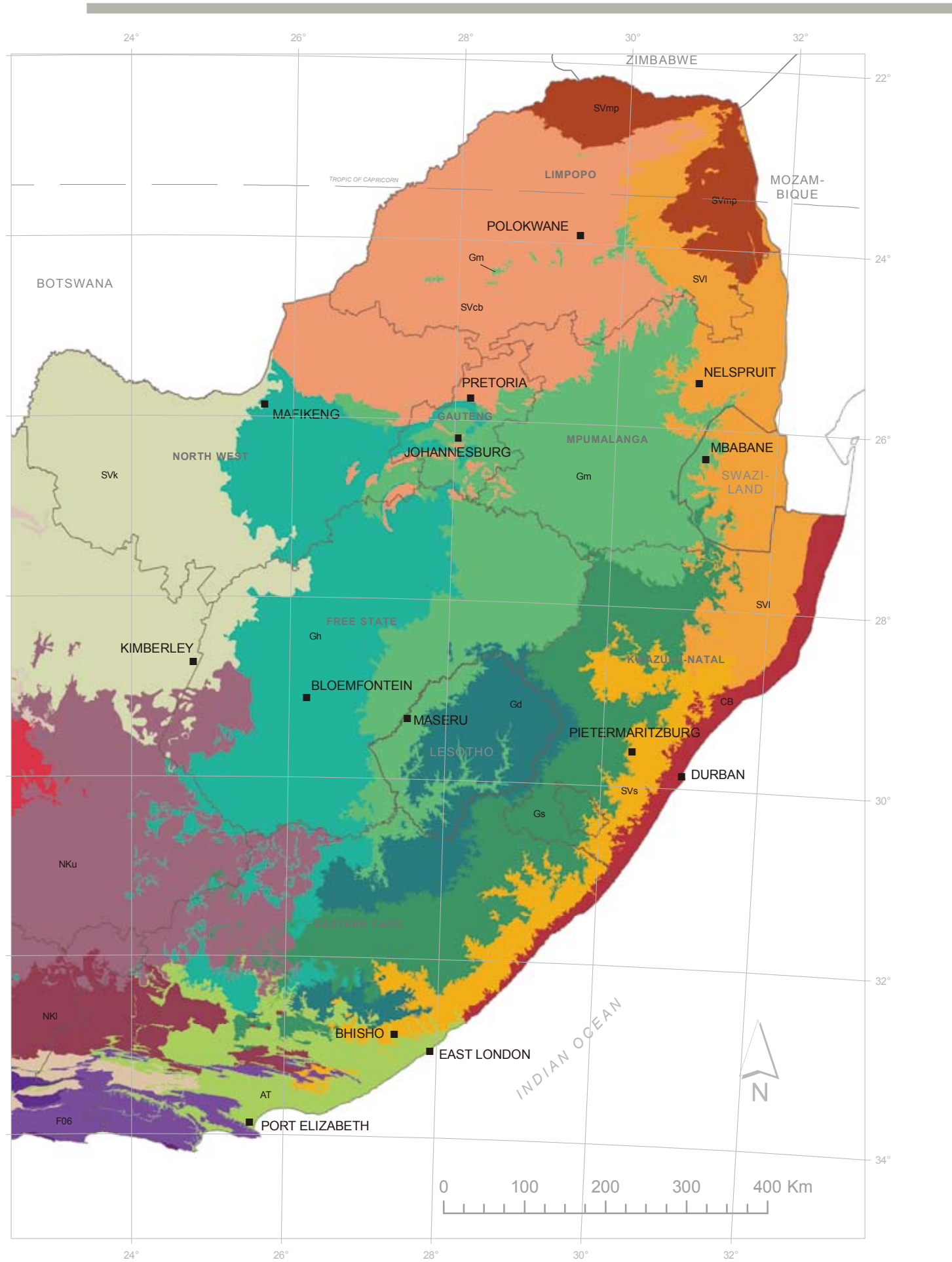


Figure 3.10 Bioregions of South Africa, Lesotho and Swaziland.



ably an approximate surrogate for animal diversity), whereas ecoregions purport to be based on plants and animals and the imprint of geological history (Olson et al. 2001). However, in mainland Africa, most of these terrestrial ecoregions were derived from the vegetation units of White (1983) with some subsequent further divisions (Burgess et al. 2004). And where widely accepted biogeographical maps were unavailable, ecoregions were delineated on the basis of land forms and vegetation (Olson et al. 2001). This supposed difference between bioregion and ecoregion in bias of the former towards plants might, therefore, turn out to be rather semantic. In the southern African context we would contend that the bioregions are better founded on floristic principles than a number of the ecoregions, although not denying the importance of some ecoregions and their informative descriptions, e.g. those ecoregions in the area corresponding to the Fynbos Biome.

The appropriateness and consistency of the geographical application of ecoregions and their affiliations within our mapping region are dealt with in the paragraphs below.

There is generally a poor correspondence between individual ecoregions and bioregions. The few exceptions include the 'Southern Africa bushveld' Ecoregion which corresponds fairly well to the Central Bushveld Bioregion (78%). There is also some correspondence between the 'Zambesian and mopane woodlands' Ecoregion and the Mopane Bioregion (60%). Otherwise, there is a close correspondence between the 'Kalahari Xeric savanna' Ecoregion and the combination of the Kalahari Duneveld and Eastern Kalahari Bushveld Bioregions (91%). These correspondences are limited to the area of our mapping domain and should the concepts tend to diverge north of this domain, the overall level of correspondence would drop, possibly to a level of poor correspondence.

Widely divergent climate can occur within a single ecoregion (Burgess et al. 2004). For example, included within the Drakensberg montane grasslands, woodlands and forests Ecoregion are both the very high-rainfall grasslands around the Drakensberg in KwaZulu-Natal and the arid grasslands on mountains around Graaff-Reinet in the Karoo. The latter arid grasslands have been more appropriately included in our Dry Highveld Grassland Bioregion. Climatic ranges within ecoregions and bioregions in general do, however, deserve further analysis.

As emerges from the above, the ecoregions of Burgess et al. (2004) for South Africa, Lesotho and Swaziland appear hierarchically diverse and can correspond at multiple levels, i.e. biome level (e.g. 'Succulent Karoo' Ecoregion and Succulent Karoo Biome), bioregion level (e.g. 'Southern Africa bushveld' Ecoregion and Central Bushveld Bioregion), and approximately at vegetation type level (i.e. 'Drakensberg alti-montane grasslands and woodlands' Ecoregion and 'Drakensberg Afroalpine Heathland vegetation type'). Through the current work we would advocate a firmly placed bioregion level which should remain hierarchically stable.

2.2 The Bioregions

The Savanna Biome (in our mapping area) contains six bioregions. The Central Bushveld Bioregion has the highest number of vegetation types and covers most of the high-lying plateau west of the main escarpment from the Magaliesberg in the south to the Soutpansberg in the north. The Mopane Bioregion has the smallest area of the bioregions in the Savanna Biome (Figure 3.11) and lies at relatively low altitude north of the Soutpansberg and on the northeastern flats of the Limpopo Province. The Lowveld Bioregion extends from the eastern foot of the Soutpansberg

southwards along the base and lower slopes of the escarpment, through the lower parts of Swaziland to the low-lying parts of Zululand in KwaZulu-Natal. The Sub-Escarpment Savanna Bioregion occurs mainly inland of the IOCB extending farther inland up major river valleys. The Eastern Kalahari Bushveld Bioregion is the largest savanna bioregion and is on average at the highest altitude (Figure 3.12). It is roughly bounded by Mafikeng, Bloemhof, Kimberley, Groblershoop and Van Zylsrus. The Kalahari Duneveld Bioregion has the fewest number of vegetation units and is typically found in the region of parallel dunes mainly in the Gordonia District north of Upington. On structural grounds (derived from satellite imagery), the Kalahari Duneveld Bioregion is, unlike the remainder of the Savanna Biome, not supported as a 'woodland biome' (Fairbanks 2000: Figure 2) and was also rejected on structural grounds as Savanna Biome in Rutherford (1997).

There are four bioregions in the Grassland Biome. The Drakensberg Grassland Bioregion is the highest-lying bioregion in the whole of our mapping area and occurs on the Lesotho highlands and immediate surrounds in KwaZulu-Natal, stretching southwards along the high-lying area of the escarpment in the Eastern Cape Province to reach the Stormberg and Amathole Mountains. It is the grassland bioregion with the fewest number of vegetation types. The Dry Highveld Grassland Bioregion constitutes the western belt (Graaff-Reinet and Aliwal North to Mafikeng) of the biome, mainly with a MAP below 600 mm. The Mesic Highveld Grassland Bioregion is the largest and has the highest number of vegetation types. It is found mainly in the higher-precipitation parts of the highveld and extends northwards along the eastern escarpment. It includes bushveld summit grasslands. The Sub-Escarpment Grassland Bioregion occurs at relatively low altitude on the plains and foothills of the Drakensberg and eastern escarpment from around Volksrus in the north to the Queenstown area in the south.

The Nama-Karoo Biome contains three bioregions, with a relatively even spread of number of vegetation types between them. The Bushmanland Bioregion occurs from the northeastern part of the Namaqualand area in the west to around Prieska in the east and from around Upington in the north to the Brandvlei/Sak River vicinity in the south. The Upper Karoo Bioregion is the largest and highest-altitude bioregion. It ranges from the eastern Calvinia District in the west to Burgersdorp in the east and from around Douglas and Petrusburg in the north to the Great Escarpment in the south. The Lower Karoo Bioregion is the smallest and at the lowest altitude. It mainly occupies the basin between the Great Escarpment in the north and the Cape Fold Mountains in the south, excluding areas of the Albany Thicket in the eastern part of the basin.

Of the two bioregions of the Desert Biome, the smaller is the Southern Namib Desert which stretches as a relatively narrow band up the valley of the Orange River from its mouth at Alexander Bay to around Sendelingsdrif. The much larger Gariiep Desert extends farther up the lower Orange River Valley at a higher altitude over rugged terrain to around Onseepkans. (See Section 2.3 of this chapter and Chapter 6 on Desert for biome level considerations of these two groupings.)

All the biome chapters following this chapter are arranged according to the bioregions as set out except for the Fynbos Biome. The text in Chapter 4 is therefore arranged rather according to substrate types, emphasising the edaphic dependences of many Fynbos types but not necessarily their climatic affiliations important in the Fynbos bioregions. The close proximity and interleaving of very different vegetation types in the Fynbos Biome posed a challenge for establishing its bioregions and in terms of our consolidation principle, we have combined

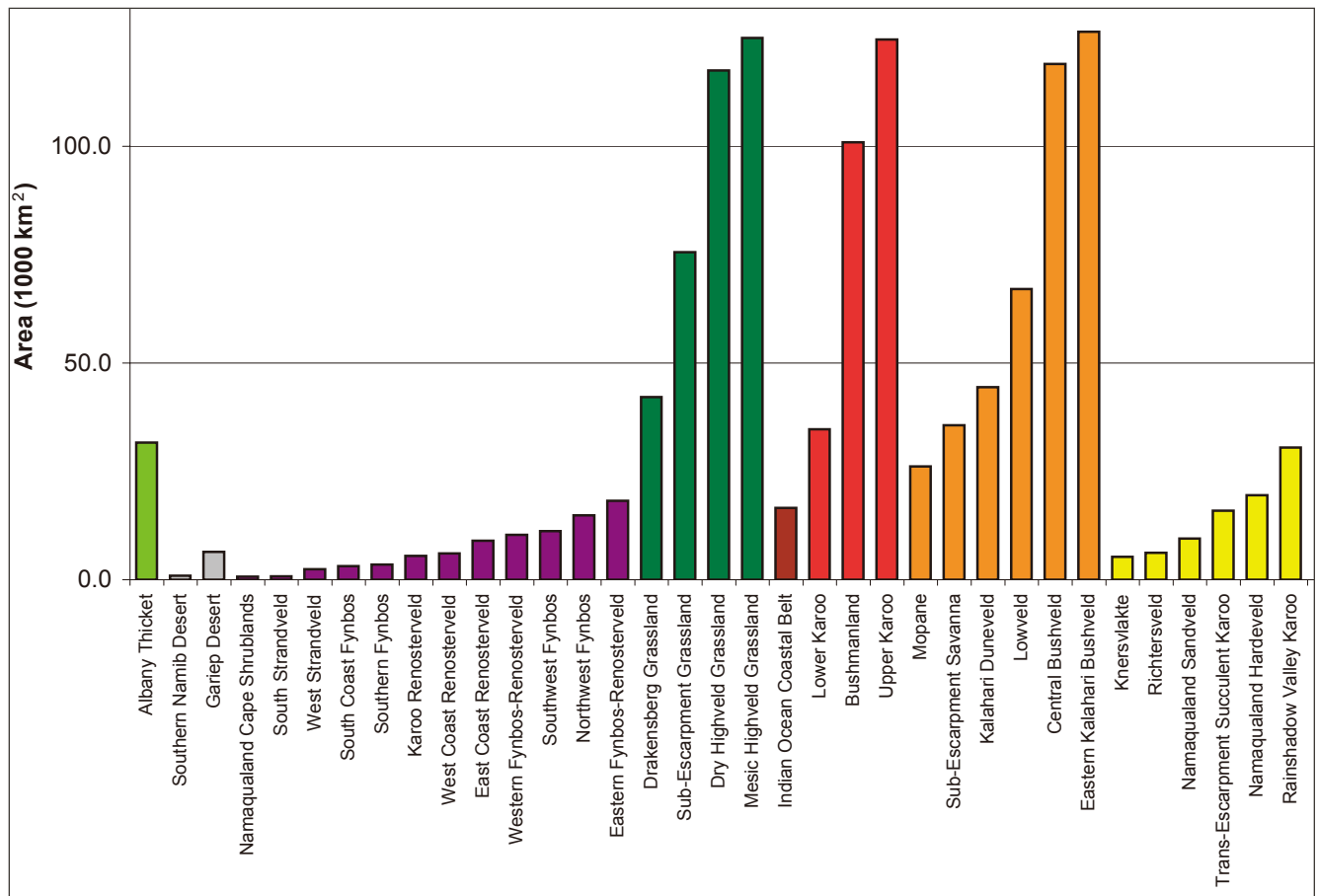


Figure 3.11 Areas of bioregions grouped according to biome.

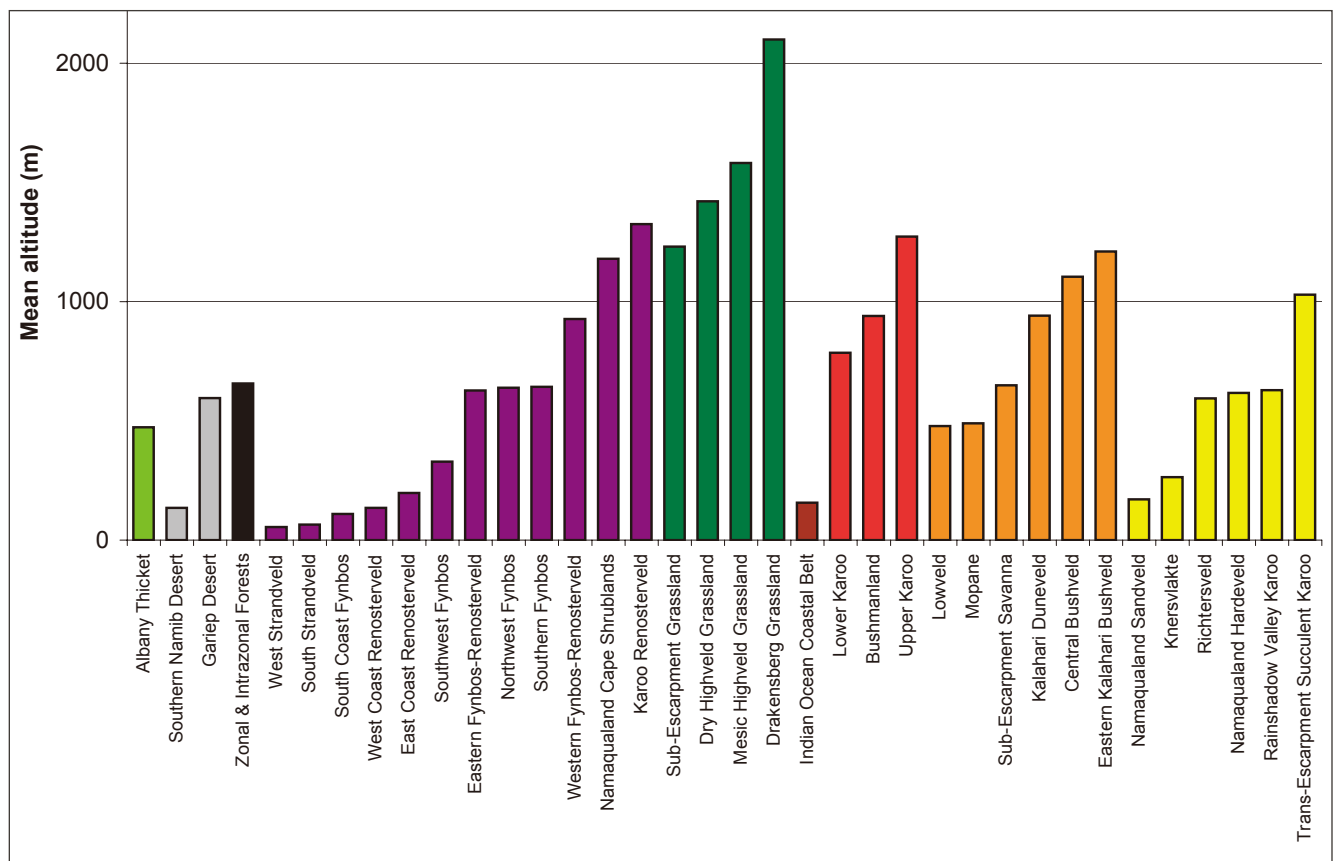
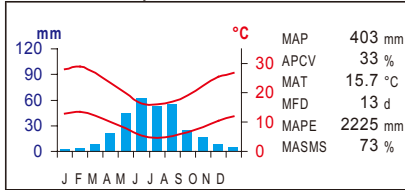
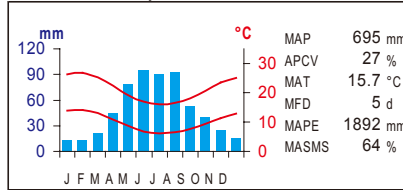


Figure 3.12 Mean altitude of bioregions grouped according to biome.

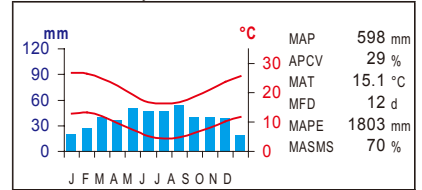
F01 Northwest Fynbos



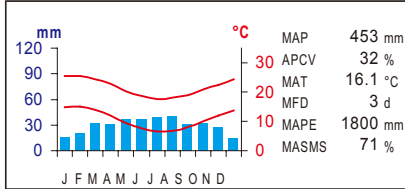
F02 Southwest Fynbos



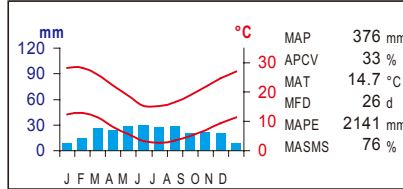
F03 Southern Fynbos



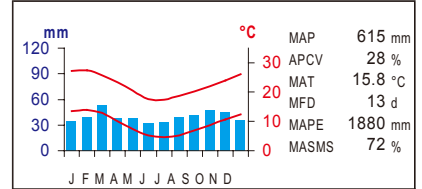
F04 South Coast Fynbos



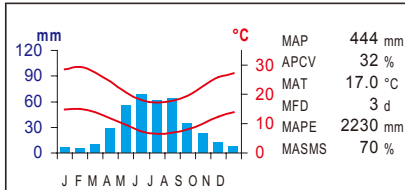
F05 Western Fynbos-Renosterveld



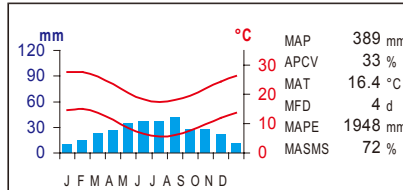
F06 Eastern Fynbos-Renosterveld



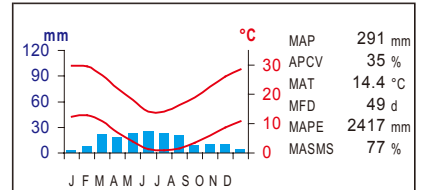
F07 West Coast Renosterveld



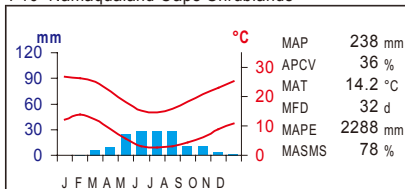
F08 East Coast Renosterveld



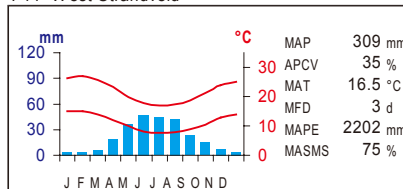
F09 Karoo Renosterveld



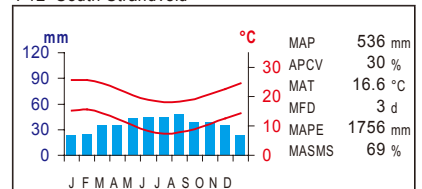
F10 Namaqualand Cape Shrublands



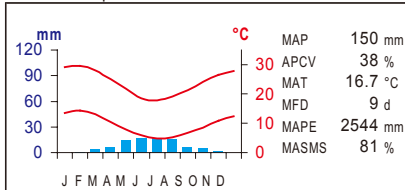
F11 West Strandveld



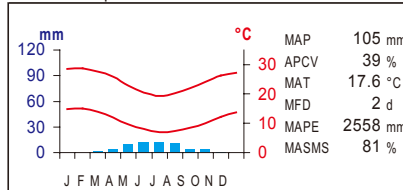
F12 South Strandveld



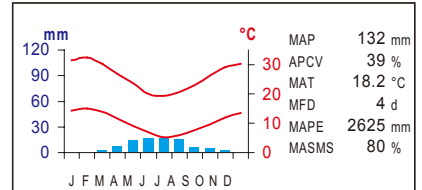
SKn Namaqualand Hardeveld



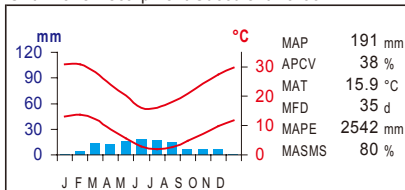
SKs Namaqualand Sandveld



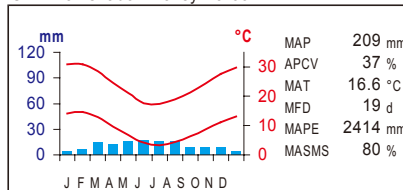
SKk Knersvlakte



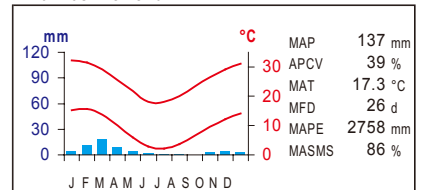
SKt Trans-Escarpment Succulent Karoo



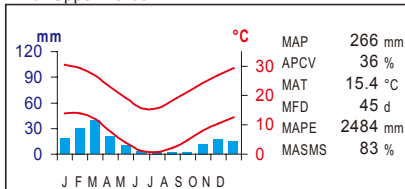
SKv Rainshadow Valley Karoo



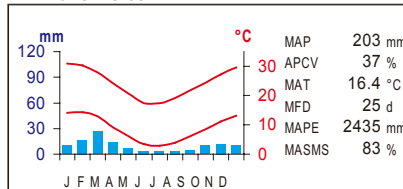
NKb Bushmanland



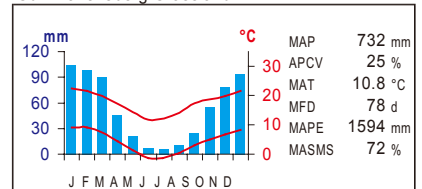
NKu Upper Karoo



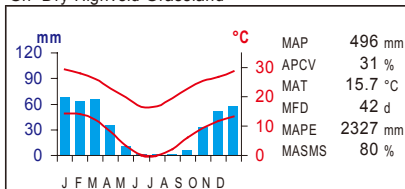
NKl Lower Karoo



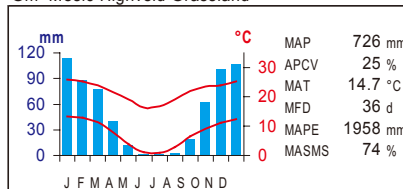
Gd Drakensberg Grassland



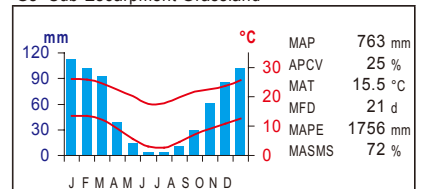
Gh Dry Highveld Grassland



Gm Mesic Highveld Grassland



Gs Sub-Escarpment Grassland



fynbos and renosterveld types in places (as have ecoregions of Burgess et al. (2004) within this biome). Thus the largest bioregion in the biome is the Eastern Fynbos-Renosterveld Bioregion which stretches from around George to Port Elizabeth and Grahamstown. To the northwest and west of this region is the Western Fynbos-Renosterveld Bioregion which mainly circumscribes the higher-elevation outcrops of fynbos in the Little Karoo from Uniondale in the east to the Touws River area in the west (except those associated with the Langeberg).

The floristic heartland of the Fynbos Biome is probably the Southwest Fynbos Bioregion. This is a sandstone (occasionally granite) and sand-defined unit and includes the mountains of the Kogelberg, Du Toitskloof area, Riviersonderend Mountains as well as the Cape Peninsula, Bredasdorp Mountains (including Potberg) and the fynbos of the sandveld on flats such as in the Hopefield District. This bioregion is flanked by two renosterveld bioregions. The West Coast Renosterveld Bioregion encompasses all the renosterveld areas to the west of the mountain chain from around Eendekuil/Piketberg in the north to Somerset West in the south. The East Coast Renosterveld Bioregion stretches from Bot River/Caledon in the west to the vicinity of Albertinia in the east and includes the renosterveld areas of the Breede River Valley. Positioned largely between the East Coast Renosterveld Bioregion and the ocean is the South Coast Fynbos Bioregion mainly on the flats between Bredasdorp and Mossel Bay. Immediately north of the East Coast Renosterveld Bioregion is the Southern Fynbos Bioregion which constitutes the sandstone mountain areas of the Langeberg from Worcester in the west to the vicinity of Herbertsdale in the east and includes higher sandstone outcrops in the Montagu area.

The second largest bioregion in the Fynbos Biome is the Northwest Fynbos Bioregion which covers the sandstone and sand areas of the biome from the Hex River Mountains in the south through the Cederberg to the Bokkeveld Escarpment near Nieuwoudtville in the north. Also included here is the Piketberg Mountain and sand patches north of Aurora on the flats to the Vredendal District and some patches northwards embedded in the Namaqualand Sandveld Bioregion of the Succulent Karoo Biome. Inland of these patches and at much higher altitudes is the smallest bioregion of the biome, namely the Namaqualand Cape Shrublands Bioregion. Most of this bioregion is centred in the Kamiesberg area of Namaqualand. The remaining two bioregions in the Fynbos Biome are strictly coastal and of very

limited area. The larger unit is the West Strandveld Bioregion which is centred in the Saldana Bay area and extends northwards to Lambert's Bay and southwards to the Cape Flats bordering False Bay. The South Strandveld Bioregion occurs in patches from Walker Bay (Hermanus) in the west to the vicinity of Oyster Bay (near Port Elizabeth) in the east.

The Succulent Karoo Biome is made up of six bioregions. The Richtersveld Bioregion covers most of the hilly and mountainous Richtersveld except for the desert areas near the Orange River. It contains the largest number of vegetation types despite having the second smallest area. The Namaqualand Hardeveld Bioregion covers much of the higher-lying hilly area between Steinkop in the north and Nuwerus in the south. To the west of this bioregion lies the Namaqualand Sandveld Bioregion, which is the lowest-lying bioregion occurring along the coastal plains from the Richtersveld in the north to the vicinity of the lower Olifants River in the south. The Knersvlakte Bioregion is the smallest bioregion and also lies at low altitude, but further inland than the last-mentioned. It is found mainly on the plains south of Kliprand in the north southwards to around Vanrhynsdorp. The Trans-Escarpment Succulent Karoo contains the fewest number of vegetation types and is the highest-lying bioregion, occurring on the upland plateau roughly from the Loeriesfontein area in the north to the vicinity of Sutherland in the south. The Rainshadow Valley Karoo Bioregion is the largest bioregion and includes the basins of the Tanqua, Robertson and Little Karoo as well as some areas north and east of the Swartberg.

2.3 Climatic Relations of Bioregions

Bioregions are divided into climatic entities with relatively similar climates within the bioregion and usually distinct climatic differences between bioregions. The following key climatic differences between the bioregions are identified.

In the Fynbos Biome, the Namaqualand Cape Shrublands Bioregion has the lowest MAP by a clear margin (Figure 3.13). The West Strandveld and Karoo Renosterveld have a similar, relatively low MAP but the former experiences almost no frost in contrast to the latter which has the highest incidence of frost in the biome. The Eastern Fynbos-Renosterveld Bioregion has the most evenly spread rainfall throughout the year. Less evenly spread rainfall is found in the Southern Fynbos, South

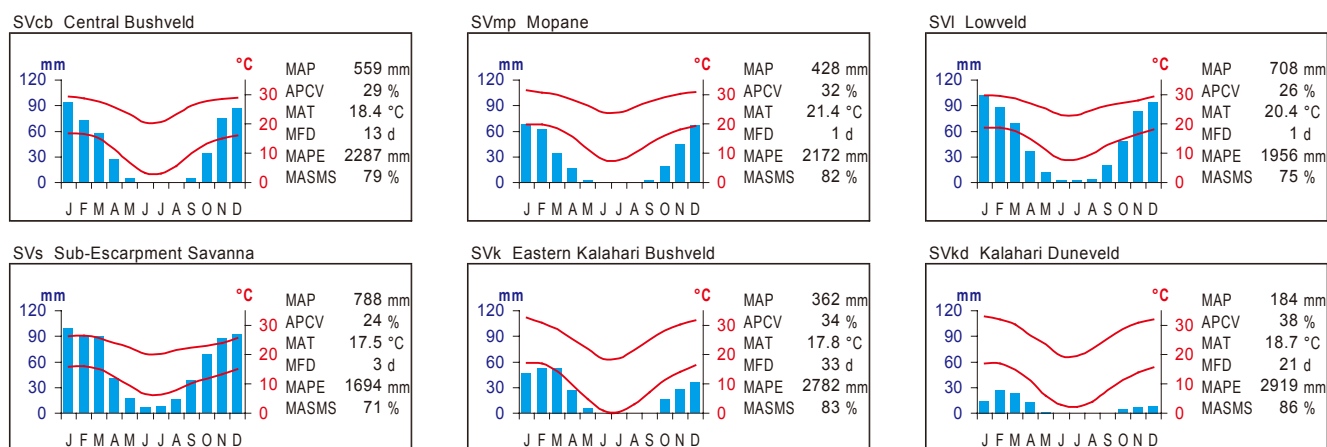


Figure 3.13 Climate diagrams of the bioregions grouped according to biome. Blue bars show the median monthly precipitation. The upper and lower red lines show the mean daily maximum and minimum temperature, respectively. MAP: Mean Annual Precipitation; APCV: Annual Precipitation Coefficient of Variation; MAT: Mean Annual Temperature; MFD: Mean Frost Days (days when screen temperature was below 0°C); MAPE: Mean Annual Potential Evaporation; MASMS: Mean Annual Soil Moisture Stress (% of days when evaporative demand was more than double the soil moisture supply).

Strandveld and South Coast Fynbos Bioregions which have a decreasing MAP in the order given. The remaining five bioregions in the biome have a clear winter-rainfall pattern with low to very low rainfall in summer. Of these, the Southwest Fynbos Bioregion has the highest MAP followed by West Coast Renosterveld, East Coast Renosterveld and Western Fynbos-Renosterveld. The Northwest Fynbos is distinguished from these last-mentioned by its high annual potential evaporation.

In the Succulent Karoo Biome, the Namaqualand Sandveld has the lowest MAP, with the Rainshadow Valley Karoo and the Trans-Escarpment Succulent Karoo Bioregions having the highest MAP. The Trans-Escarpment Succulent Karoo has a much higher incidence of frost than the Rainshadow Valley Karoo. This incidence of frost approaches that of the adjacent Nama-Karoo Biome. The Namaqualand Hardeveld Bioregion has lower temperatures and more frost days than the Knersvlakte Bioregion. Climatic data for the Richtersveld Bioregion are too sparse to make specific comparisons with the other bioregions.

The Southern Namib Desert has a clear winter rainfall and relatively 'reliable' pattern of frequent fog in contrast to the Gariep Desert with precipitation ranging from even less predictable rainfall transitional between winter and summer to clearly summer-autumn rainfall; it experiences no fog. The effects of these climatic differences are so profound that these bioregions could probably each be raised to the level of biome. In the Nama-Karoo, the Bushmanland Bioregion has considerably lower MAP than the other two bioregions. Of the other bioregions, the Upper Karoo Bioregion has about twice as much frost as the Lower Karoo.

Within the Grassland Biome, the Drakensberg Grassland Bioregion has much lower temperatures, with a high incidence of frost compared to the other grassland bioregions. Dry Highveld Grassland has significantly lower precipitation than Mesic Highveld Grassland. Although MAP is similar between Mesic Highveld Grassland and Sub-Escarpment Grassland, the latter differs in its higher temperatures and fewer frost days.

In the Savanna Biome, the two bioregions with the highest MAP are the Sub-Escarpment Savanna and Lowveld, with the latter experiencing a significantly greater annual potential evaporation. The Kalahari Duneveld Bioregion has by far the lowest MAP in the biome. The Eastern Kalahari Bushveld Bioregion has more than twice as much frost as the Central Bushveld Bioregion while the Mopane Bioregion experiences virtually no frost.

It should be clear that the climatic relations indicated above represent climatic averages within a unit and, therefore, the overall trends and these averages do not address the spatial range of climate within a unit.

3. Credits

M.C. Rutherford wrote the text which was edited by L. Mucina who also added sections 1.1 and 1.7 which were in turn edited by M.C. Rutherford. L.W. Powrie was responsible for the technical compilation of the material for the figures and the tables (except for Table 3.5 supplied by L. Mucina). M.C. Rutherford and L.W. Powrie performed the decision tree analyses and W. Thuiller (now Grenoble, France) assisted with the CART decision tree. Data for the climate diagrams were taken or derived from the work of R.E. Schulze. This chapter is directed mainly at comparisons between biomes and between bioregions but we fully acknowledge the individual contributions to biome and bioregion boundaries supplied by the authors of the individual

biome chapters in this book (see Credits at the end of each major chapter).

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