Chapter 2 Angola in Outline: Physiography, Climate and Patterns of Biodiversity



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Abstract Angola is a large country of 1,246,700 km² on the southwest coast of Africa. The key features of the country's diverse geomorphological, geological, pedological, climatic and biotic characteristics are presented. These range from the ultra-desert of the Namib, through arid savannas of the coastal plains to a biologically diverse transition up the steep western Angolan Escarpment. Congolian rainforests are found in Cabinda and along the northern border with the Democratic Republic of Congo, with outliers penetrating southwards along the Angolan Escarpment, or up the tributaries of the Congo Basin. Above the escarpment, high mountains rise to 2620 m above sea level, with isolated remnants of Afromontane forests and grasslands. Extensive Brachystegia/Julbernardia miombo moist woodlands dominate the plateaus and peneplains of the Congo and Zambezi basins, and dry woodlands of Colophospermum/Acacia occur in the southeast towards the Cunene River, with Baikiaea/Burkea/Guibourtia woodlands dominating the Kalahari sands of the endorheic basins of the Cubango and Cuvelai rivers. Rainfall varies from lower than 20 mm per year in the southwest to over 1600 mm in the northwest and northeast. At a regional scale, Angola is notable for having representatives of seven of Africa's nine biomes, and 15 of the continent's ecoregions, placing Angola second only after South Africa for its diversity of African ecoregions.

Keywords Afromontane forest · Biogeography · Biomes · Climate change · Congolian forest · Ecoregions · Namib · Kalahari Basin · Zambezian savannas

Introduction

This chapter presents a general outline of the physical geography and biodiversity characteristics of Angola, as background to the chapters that follow. It draws on the work of the great Portuguese agro-ecologist Alberto Castanheira Diniz, who

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synthesised the diverse drivers of Angola's ecological systems and agricultural potential, based on his many decades of fieldwork in the country (Diniz and Aguiar 1966; Diniz 1973, 1991, 2006). Colonial records of climatic variables (Silveira 1967) are used in the absence of recent time series. The pioneer studies on Angolan vegetation by Gossweiler and Mendonça (1939) and Barbosa (1970) are fundamental to any account on Angola biodiversity. Surveys of Angola's protected areas and biodiversity 'hotspots' (Huntley 1974a, b, 2010, 2015, 2017) provide conservation context. This outline also draws on the recent regional geographies of Angola by Mendelsohn and co-workers (Mendelsohn et al. 2013; Mendelsohn and Weber 2013, 2015; Mendelsohn and Mendelsohn 2018). The chapter is also strengthened by material detailed in the specialist papers that form the core of this volume.

Location and Extent

As a large country of 1,246,700 km² on the southwest coast of Africa, Angola is roughly square in outline, lying between 4° 22′ and 18° 02′ south latitude, and 11° 41′ and 24° 05′ east longitude. It is bounded to the west by an arid 1600 km coast-line along the Atlantic Ocean; to the north by the moist forest and savanna ecosystems of the Republic of Congo and the Democratic Republic of Congo (DRC); to the east by the moist savanna and woodland ecosystems of the DRC and Zambia; and by arid woodlands, savannas and desert along its 1200 km southern border with Namibia.

Geomorphology and Landscape Evolution

The general topography of Angola is illustrated in Fig. 2.1. In summary, coastal lowlands lying below 200 m altitude and of 10–150 km breadth occupy 5% of the country's land surface area, leading to a stepped and mountainous escarpment rising to 1000 m (23%), and an extensive interior plateau of 1000–1500 m (65%). Seven percent of the country lies above 1500 m, reaching its highest point at 2620 m on Mount Moco.

The ecological importance of the major physiographic divisions in Angola was recognised as early as the 1850s by the pioneer Austrian botanist Friedrich Welwitsch who categorised the 5000 plant species that he collected in Angola within three regions: região litoral, região montanhosa, and região alto-plano (Welwitsch 1859). Besides his remarkable contribution to the founding of Angolan botany, Welwitsch prepared detailed geological profiles across the landscapes inland of Luanda and Moçâmedes (Albuquerque and Figueirôa 2018), probably the first such analyses in western Africa (Fig. 2.2). His understanding of the patterns and relationships of geology, physiography and vegetation set a strong ecological tradition that has been followed by successive students of Angola's biodiversity.

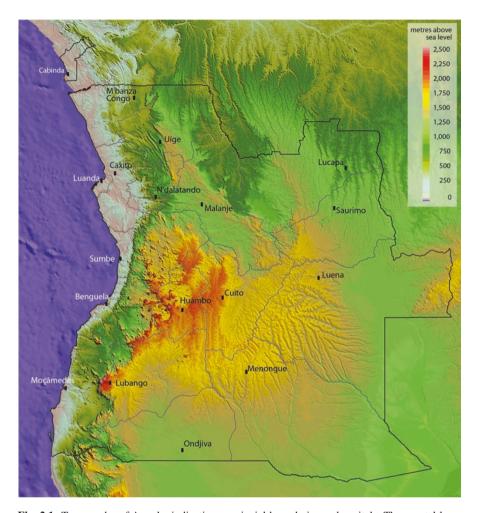


Fig. 2.1 Topography of Angola, indicating provincial boundaries and capitals. The coastal low-lands, western escarpments, central highlands and plateaus, and the major drainage basins of the Cuanza, Congo and Zambezi rivers are clearly revealed

A further detailed and indeed classic study of Angola's geomorphology and local ecology was that of the German geographer Otto Jessen (1936). Jessen undertook a series of 11 transects from the coast inland, traversing the escarpment to the interior plateau from Moçâmedes and thereafter at intervals northwards to Luanda. Describing, illustrating and mapping selected vegetation communities, geological exposures, landscapes, landuse and ethnological features of the country, Jessen's Angolan work remains unique in its diversity of interest and originality. He recognised five major erosional planation surfaces in western Angola at a time when geomorphology was evolving as a discipline, and he was recognised by King (1962) as one of the founders of peneplanation theory. Geomorphological studies in Angola



Profil idéal des terrains, de Loanda á Quisonde, commençant au 9º degré de latitude sud et s'infléchissant jusqu'au 10º.

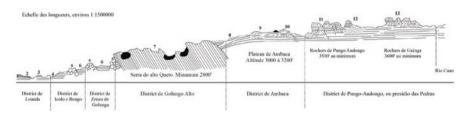


Fig. 2.2 Geological profile from Luanda to Quisonde, scanned from the original manuscript produced by Friedrich Welwitsch during his expeditions between 1853 and 1860. The lower profile is a redrafted version of the upper profile adapted from Choffat (1888), and reproduced with permission from Albuquerque and Figueirôa (2018) and of the Museums of the University of Lisbon Historical Archives

continued from the 1950s to 1970s by Portuguese researchers, including Marques (1963), Feio (1964) and Amaral (1969), whose work is summarised by Costa (2006).

More recent research, in particular that on the evolution and of the major tectonic and erosional patterns across southern Africa (Cotterill 2010, 2015; Cotterill and De Wit 2011) and on the biogeography of the freshwater fishes of Angola (Skelton 2019) provide a picture of a very dynamic landscape since the breakup of Gondwana in the late Cretaceous. These and other authors are providing an improved understanding of the processes of uplift, back-tilting, down-warping, deposition, erosion and river capture on the evolution of the Kalahari Basin. The impacts of sea-level fluctuations and of the flow of the Congo River on coastal waters and on the erosional forces of the Congo Basin as it impacts on the Zambezi Basin are guiding our interpretation of the dramatic events shaping the faunal and floral patterns of today. Cotterill (2015) presents a synthesis of hypotheses on the evolution of the Kalahari from the late Mesozoic into the early Cenozoic, events which were followed by the later overlying suite of younger Kalahari sediments – the world's largest sandsea. The interplay of geological and paleoclimatic drivers described by Cotterill (2010, 2015), through the pulsing of hot wet and cool dry episodes during the Plio-Pleistocene, was accompanied by the expansion and contraction of forest and savanna habitats responding to climatic and fire regimes.

The role of fire in shaping the landscapes of Angola – and particularly of the dominant miombo moist savanna biome – has become a topic of discussion in recent years (Zigelski et al. 2019). Maurin et al. (2014) provide evidence based on the dated phylogenies of 1400 woody species to support the proposal that the 'underground forests' (White 1976) that are so prominent across the moist miombo savannas and woodlands of the south-central African plateau, evolved in response to high fire frequency. They suggest that moist savannas pre-date the emergence of anthropogenic fire and deforestation, becoming a prominent component of tropical vegetation from the late Miocene (ca. 8 Ma). Maurin et al. (2014) conclude that the evolution of geoxyles ('underground trees') that characterise these moist savannas define the timing of the transition to fire-maintained savannas occurring in climates suitable for and previously occupied by forests. The further interpretation of these key drivers of evolution processes is fundamental to an improved understanding of the biogeography of Angola.

A major contribution towards an ecological understanding Angola's contemporary landscapes and natural regions, and their agro-forestry potential, was that of Castanheira Diniz. Diniz (Diniz and Aguiar 1966, Diniz 1973, 1991) provides a series of maps illustrating the key features of Angola's topography, geomorphology, geology, climate, soils, and phyto-geographic and bio-climatic zones. Diniz's 11 'mesological' units (Fig. 2.3) provide a useful framework for discussions on Angola's ecology and biodiversity. Indeed his mesological concept closely corresponds with current perceptions of ecoregions. He also delineated and described 32 agro-ecological zones (Diniz 2006). Although some of his 11 mesological units need more rigorous and objective definition and delineation, they have become widely adopted within Angola. Important aspects of these 11 broad units will be summarised here, integrating these with insights from other sources.

1. Coastal Belt (Faixa litoranea sensu Diniz). This is a mostly continuous platform at 10–200 m above sea level, broken occasionally by broad river valleys. In contrast to the situation on the east coast of Africa at similar latitudes, the Angolan coastline is notable for the absence of coral reefs and coastal dune forests. Long sandbars stretch northwards from rivers such as the Cunene and Cuanza. Mudflats and mangroves occur at most river mouths from Lobito northwards, increasing in dimension and diversity towards the Congo. Much of the coast is uplifted, resulting in sharp sea-cliffs of 10-100 m. In places as narrow as 10 km, the coastal belt is mostly of about 40 km width, broadening to 150 km northwards of Sumbe and up the lower Cuanza. The coastal plains are composed mostly of fossiliferous marine sediments of the Cabinda, Cuanza, Benguela and Namibe geological basins. The northern coastal platforms are covered by deep red Pleistocene sands (terras de musseque) of former beaches. Lying below the sands, and exposed over large areas, are Cretaceous to Miocene clays, gypsipherous marls, dolomitic limestones and sandstones. Important beds of Cretaceous fossils occur at Bentiaba and Iembe, the latter including the sauropod dinosaur Angolatitan adamastor (Mateus et al. 2011, 2019). The

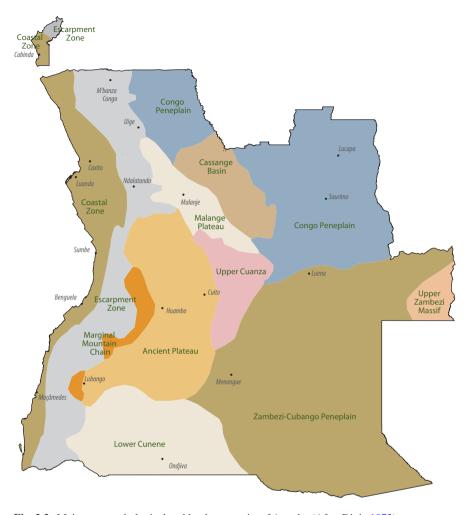


Fig. 2.3 Main geomorphological and landscape units of Angola. (After Diniz 1973)

- southernmost segment of the Coastal Belt includes the mobile and mostly vegetation-less dunes of the Namib Desert.
- 2. Escarpment Zone (Faixa subplanaltica sensu Diniz; região montanhosa sensu Welwitsch). A broad transition belt lies between the coastal plains and the interior plateaus variable in breadth and gradient. Over much of the zone, the transition advances up several steep steps of between 400 and 600 m. In the south, between Moçâmedes and Lubango, the escarpment of the Serra da Chela is very sharp, rising 1000 m at Tundavala and Bimbe. The geology of the Escarpment Zone is complex, comprising crystalline rocks of the Precambrian: granites, gneisses, schists, quartzites and amphibolites. The Escarpment Zone (also referred to as the Western Angolan Scarp) includes very hilly country,

- with mountainous belts in the north, and some major inselbergs in the south, the most important of which is Serra de Neve, which rises to 2489 m from the surrounding plains and low hills. The Angolan Escarpment has long been recognised for its biogeographic importance (Humbert 1940, Hall 1960a, Huntley 1974a) and has been the centre of interest of many recent studies (Hawkins 1993, Dean 2000, Mills 2010, Cáceres et al. 2015, 2017).
- 3. Marginal Mountain Chain (*Cadeia Marginal de Montanhas* sensu *Diniz*). Residual mountain lands, mostly at 1800–2200 m, underlain mostly by Precambrian rocks such as gneiss, granites and migmatites, lie at the western margin of the extensive interior plateau, and are known as the Benguela, Huambo and Huíla Highlands. The highest peaks rise to 2420 m on Mount Namba, 2582 m on Serra Mepo and 2620 m at Mount Moco. The mountains are of biogeographic importance for their montane grasslands, with some elements of the Cape flora, and relict patches of Afromontane forests and endemic bird assemblages (Humbert 1940; Hall 1960b; Hall and Moreau 1962; Huntley and Matos 1994; Dean 2000; Mills et al. 2011, 2013; Vaz da Silva 2015).
- 4. Ancient Plateau (*Planalto Antigo*). This extensive plateau drops eastwards from below the Marginal Mountain Chain and encompasses the headwaters of the Cunene, Cubango, Queve and Cutato rivers, comprising rolling landscapes with wetlands and low ridges with scattered granitic inselbergs. It drops from 1800 m in the west to 1400 m in central Angola.
- 5. Lower Cunene (*Baixo Cunene*). This is a rather artificial unit, leading imperceptibly down from 1400 m on the 'Ancient Plateau' to the frontier with Namibia at 1000 m. The gentle gradient of the eastern half forms the very clearly defined Cuvelai Basin, which drains as an ephemeral catchment into the Etosha Pan. West of the Cunene the landscape is more broken, with pockets of Kalahari sands between low rocky hills.
- 6. Upper Cuanza (*Alto Cuanza*). The upper catchments of the Cuanza and its tributary the Luando, at altitudes between 1200 and 1500 m, form a distinct basin of slow drainage feeding extensive wetlands during the rain season.
- 7. Malange Plateau (*Planalto de Malange*). A gently undulating plateau at 1000–1250 m, dropping abruptly, on its northeastern margin, some several hundred metres to the *Baixa de Cassange* and the Cuango drainage. The escarpment ravines hold important moist forest outliers (such as at Tala Mungongo) that deserve investigation. To the west, the plateau is drained by the rivers flowing to the Atlantic, most spectacularly by a tributary of the Cuanza, the Lucala, that drops over 100 m at the famous Calandula Falls (formerly Duque da Bragança Falls).
- 8. Congo Peneplain (*Peneplanície do Zaire*). This is a vast sandy peneplain, drained by the northward flowing tributaries of the Cassai/Congo Basin, and stretching eastwards from the margins of the mountainous northern end of the Escarpment Zone in Uíge, to the extensive *Chanas da Borracha* of the Lundas. These gently dipping plains, mostly at 1100–800 m, are being aggressively dissected by the many northward flowing, parallel tributaries of the Congo Basin. The Cuango River, draining the *Baixa de Cassange*, drops to 500 m at the

- frontier with the Democratic Republic of Congo. The southern boundary of this Congo Peneplain is defined imperceptibly by the watershed between the Zambezi and Congo basins, lying at ca. 1200 m.
- 9. Cassange Basin (*Baixa de Cassange*). A wide depression, several hundred metres below the surrounding plateaus, is demarcated by abrupt escarpments to the west and the densely dendritic catchment of the Cuango to the northeast. The geological substrate comprises Triassic Karoo Supergroup sediments of limestone, sandstone and conglomerates. Within the Basin, several large tablelands remnants of the old planation surface rise above the depression as extensive plateaus flanked by sheer, 300 m escarpments, exemplified by Serra Mbango, which awaits biological survey.
- 10. Zambezi-Cubango Peneplain (*Peneplanície do Zambeze-Cubango*). This is the vast peneplain draining deep Kalahari sands, with slow-flowing rivers that meander across the gently dipping plateau from 1200 m at the watershed with the Congo Basin to 1000 m at the frontier with Namibia. Within this extensive peneplain, the Bulozi Floodplain occupies an area in excess of 150,000 km² in Angola and Zambia.
- 11. Upper Zambezi Massif (*Maciço do Alto Zambeze*). The Calunda Mountains of eastern Moxico, composed of Precambrian schists and norites, dolorites, sandstones and limestones, rise to 1628 m above the Zambezi peneplain which lies at 1150 m. The mountains form a striking contrast to the almost featureless landscape that stretches some 800 km eastwards from Huambo to Calunda.

Rivers and Hydrology

Angolan river systems fall into two categories. First, coastal rivers drain the central and western highlands and flow rapidly westwards where they have penetrated the steep escarpment to the Atlantic Ocean. Most of these coastal rivers are relatively short, are highly erosive and carry high sediment loads. Backward erosion by some of these has produced minor basins, such as the amphitheatres of the upper Queve and Catumbela. The biogeographic importance of the river captures associated with these systems, especially the Congo, Cuanza, and Cunene, have been profound, as described by Skelton (2019). Most of the coastal rivers south of Benguela are ephemeral.

The second major category of river systems is that of the vast interior plateaus. Drained by nine large hydrographic basins, seven of which are transnational, Angola serves as the 'water tower' for much of southern and central Africa. Many of these rivers arise in close proximity on either side of the gently undulating watershed between the Cuanza, Cassai (Congo), Lungue-Bungo (Zambezi), Cunene, and endorheic Cubango (Okavango) basins. These rivers drain the vast and deep Kalahari sands, are slow moving and due to the filtering action of the sands, are crystal clear and nutrient poor. A separate ephemeral, endorheic system, the Cuvelai Basin, drains southwards into the Etosha Pan.

The conservation importance of the Angolan river systems is of great significance, feeding as they do two wetlands (Okavango and Etosha) of global importance, and the still under-researched Bulozi Floodplain of Moxico. This is possibly the largest ephemeral floodplain in Africa – 800 km from north to south and 200 km from east to west – straddling the Angola/Zambia frontier (Mendelsohn and Weber 2015).

Geology and Soils

The geological history and soil genesis of Angola is complex and interrelated, and influenced by rainfall, drainage, evaporation and wind. Mateus et al. (2019) provide a map and stratigraphic profile of the geology of Angola which summarises the major geological features of the country. The predominance of a broad belt of Precambrian systems along the western margin of the country, with Cenozoic systems occupying most of the eastern half, is striking. Over three-quarters of the country (Fig. 2.4) is covered by two main soil groups arenosols and ferralsols – an understanding of which provides an essential introduction to Angolan pedology. For simplicity, soils will be described with reference to their geological substrate.

First, Angola's main soil groups are the sandy arenosols (*solos psamíticos*) that cover more than 53% of the country. These sands are dominant features of three major landscapes: the dunes of the Namib Desert; the red '*terras de musseque*' of the coastal belt northwards from Sumbe; and the vast Kalahari Basin. The great majority of the arenosols lie to the east of approximately 18° longitude – the aeolian sands of the Kalahari Basin which cover nearly 50% of Angola and hides nearly all of the underlying geological formations. The Kalahari Basin, extending across 2500 km from the Cape in the south to the Congo Basin in the north, and up to 1500 km in breadth, is reputedly the largest body of sand in the world. The sands have been deposited by wind and water over the past 65 million years. Composed of quartz grains that hold no mineral nutrients, and with very little accumulated organic matter, they are thus of very low fertility and water-holding capacity. Waters passing through the vast catchments of the Congo, Cubango and Zambezi basins that drain the Kalahari are therefore extremely pure.

Second, the higher ground of the western half of Angola (the Ancient Massif) is dominated by ferralsols (*solos ferralíticos*) derived from underlying rocks (gneisses, granites, metamorphosed sediments of the Precambrian Basement Complex; and schists, limestones and quartzites of the West Congo System). Ferralsols cover approximately 23% of Angola. The soils are mostly of low water-holding capacity. Because they are heavily leached in higher rainfall areas, the loss of mineral nutrients and organic matter results in low fertility. They are characteristically reddish due to the oxidation of their high iron and aluminium content, which also accounts for the presence in many areas of ferricrete hardpan horizons a metre or two below the surface, impeding root and water penetration and resulting in the formation of extensive areas of laterite.

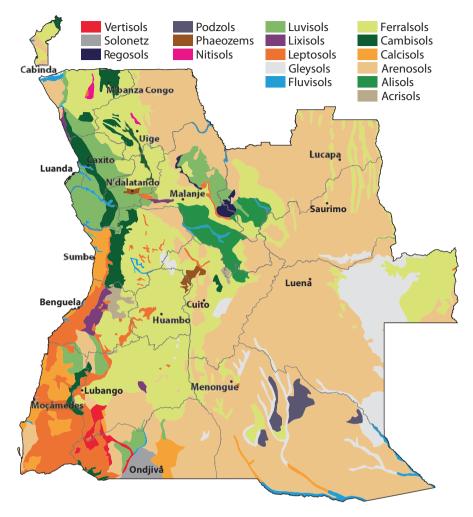


Fig. 2.4 Outline of the main soil types of Angola (from Jones et al. 2013), illustrating the predominance of arenosols in the eastern half of the country, and ferralsols across the western and central plateaus

These two low-fertility soil groups (arenosols and ferralsols) cover over 76% of the country, thus despite the adequacy of rainfall over most of Angola, agricultural production faces the challenges of low soil fertility (Neto et al. 2006; Ucuassapi and Dias 2006). The natural vegetation types that cover both arenosols and ferralsols – predominantly miombo woodlands – are well adapted to these soil conditions and the untransformed landscape gives the appearance of great vitality and luxuriance.

The next soil grouping in terms of landcover, occupying 6% of Angola, are the shallow regosols (*litosolos*) of rocky hills and gravel plains, most extensive in the arid southwest. Other important soil types include luvisols, calcisols and cambisols (*solos calcários, solos calcialíticos*), which provide fertile loam soils for crops

(including the 'coffee forests' of the Escarpment Zone); alluvial fluvisols (*solos aluvionais*) in drainage lines with high organic content and high water retaining capacity, suitable for crops if not water-logged; gleysol clays (*solos hidromórficos*), typically acidic and waterlogged and occasionally very extensive – as on seasonally flooded plains such as Bulozi Floodplains.

Climate and Weather

The diverse climatic and weather conditions experienced across Angola result from many atmospheric, oceanic and topographic driving forces.

First, the geographic position of Angola, stretching from near the Equator to close to the Tropic of Capricorn, across 14 degrees of latitude, accounts for the overall decrease in solar radiation received and thus annual mean temperatures experienced from north to south. The latitudinal decrease in mean annual temperature is illustrated by data from stations in the hot northwest and northeast (Cabinda: 24.7 °C; Dundo: 24.6 °C), compared with stations in the milder southwest and southeast (Moçâmedes: 20.0 °C; Cuangar: 20.7 °C).

Secondly, both temperature and precipitation are influenced by altitude. The decrease in mean annual temperature can be illustrated from sites below the Chela escarpment to the highest weather station in the country: i.e. from Chingoroi: altitude 818 m, mean annual temperature 23.1 °C; Jau: altitude 1700 m, mean annual temperature 18.0 °C; and finally Humpata-Zootécnica: altitude 2300 m, mean annual temperature 14.6 °C.

Thirdly, and of greatest importance to the rainfall patterns that determine vegetation and habitat structure, are the influences of the atmospheric systems which dominate central and southern Africa. Circling the globe near the Equator is a belt of low pressure where the trade winds of both Northern and Southern Hemispheres converge, creating strong convective activity which generates the dramatic thunderstorms that characterise the inter-tropics. Known as the Inter-tropical Convergence Zone (ITCZ), the belt moves southwards over Angola during summer, and then returns northwards to the Equator as winter approaches. The rainfall season that is triggered by the ITCZ passes across northern Angola from early summer, reaching southern Angola in late summer. The climate is strongly seasonal, with hot wet summers (October to May) and mild to cool dry winters (June to September). Some stations in northern Angola receive two peaks of rainfall, early summer and late summer, often with a short drier period in mid-summer.

Moving in tandem with the ITCZ are two high-pressure systems – over the Atlantic and over southern Africa – the South Atlantic Anticyclone and the Botswana Anticyclone. In simple terms, these two anticyclones block the southward movement of moist air from the ITCZ during winter (preventing cloud formation) and as the high-pressure cells move southwards in summer, the conditions required for cloud formation return. This pulsing of rainfall systems is clearly illustrated in the series of rainfall maps prepared by Mendelsohn et al. (2013) from weather satellite imagery (Fig. 2.5).

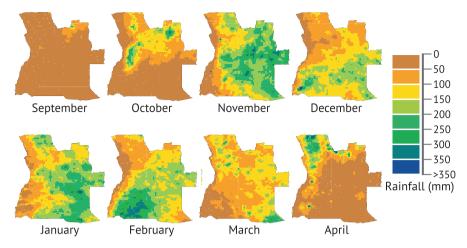


Fig. 2.5 The impact of the southwards and northwards pulsing of the Inter-tropical Convergence Zone on rainfall seasonality across Angola during 2009/2010. (From Mendelsohn et al. 2013)

During winter and early summer, the Botswana Anticyclone generates strong winds that blow across Angola from east to west, with impacts on micro-relief over much of the country. In the southwest, the winds pick up dust from the arid lands and create hot, choking dust storms that feed the sand dunes of the Namib. The winds are also notorious in the north, where they desiccate the grasslands of the Lundas. In the east, the winds and their sand deposits account for dune formation across the Bulozi Floodplain (Mendelsohn and Weber 2015).

Rainfall and temperature seasonality and other climatic parameters are illustrated by the climate diagrams in Fig. 2.6. The distribution of mean annual rainfall across Angola is summarised in Fig. 2.7.

Fourthly, as noted above, altitude and seasonality determine temperature conditions. However, an anomaly to this general rule occurs in the coastal belt of Angola, especially in the far south, through the influence of the temperature inversion created by the cold, upwelling Benguela Current. The Benguela Current has a stabilizing effect on the lower atmosphere and prevents the upward movement of moist, cloud-forming air off the ocean, accounting for the evolution of the Namib Desert. Its impact also extends as far north as Cabinda, where a narrow belt of arid savanna woodland and dry forest, of acacias, sterculias and baobabs, flanks the rainforests of the Maiombe.

Despite the aridity of the coastal zone, the cooling effect of the Benguela Current results in low stratus cloud and fog (*cacimbo*) through much of winter, with heavy dew condensing on vegetation along the coast even during the driest months of winter. The fog belt is most pronounced between Moçâmedes and Benguela, where epiphytic lichens reach great abundance in an otherwise desertic environment. The Benguela Current also results in a gradient of increasing precipitation from south to north and from west to east. The rainfall gradients are locally accentuated by the orographic influence of the escarpment and the highland mountain massifs. The

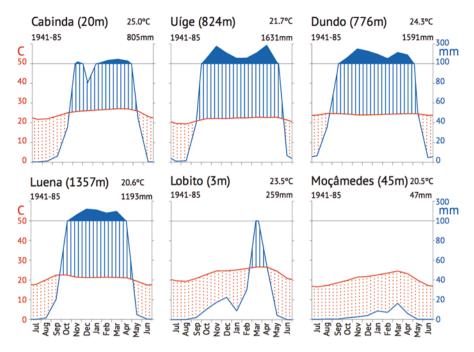


Fig. 2.6 Climate diagrams illustrating rainfall and temperature seasonality and other climatic parameters. Note weak bimodal rainfall maxima for stations in northern Angola and unimodal maxima in central and southern Angola

sharp relief of the escarpment creates conditions for orographic rainfall along most of this zone, supporting the 'coffee forests' of Seles, Gabela, Cuanza-Norte and Uíge.

Attempts to synthesise climatic characteristics into simple formulae or graphics have resulted in a wide range of classification systems. A synthesis of climatic data provided by the widely used Köppen and Thornthwaite classification systems was undertaken by Azevedo (1972) to map and quantify, at a national scale, the climatic regions of Angola, based on the substantial data set available at that time. Interestingly, despite some of its shortcomings, the Azevedo map provides a closer fit with general features of Angola's bio-climatic patterns than a much more recent map (Peel et al. 2007). The latter map is based on a global synthesis and review of the Köppen system, and draws on a very limited data set for Angola (5 stations for temperature; 16 stations for precipitation). The northern region of Angola is typical of Köppen's Tropical Wet Savanna (Aw) group, the plateau of the Temperate Mesothermal (Cw) group, and the southwest and coastal plain the Dry Desert and Semi-desert (Bsh, Bwh) group.

Mean annual rainfall and mean monthly temperatures for hottest and coldest months illustrate a few climatic characteristics of the Köppen regions (Table 2.1). The absence of data on extreme minimum temperatures and of frost occurrence is regrettable, as these factors, in tandem with fires and herbivory, play significant roles in the floristic composition and physiognomic structure of Angolan vegetation (Zigelski et al. 2019).

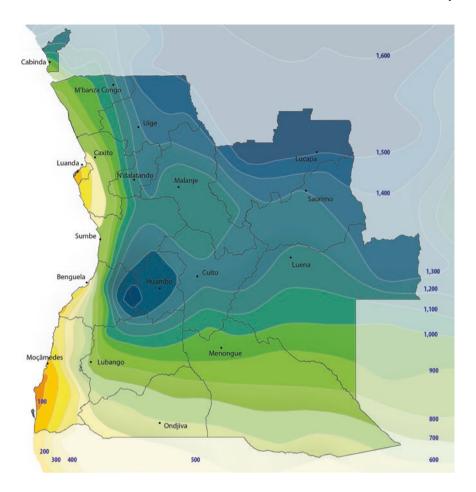


Fig. 2.7 Mean annual rainfall in Angola

Climate Change

Studies on the climate of Angola have been frustrated in recent years by the collapse of the extensive network of weather stations maintained during the colonial era by the then Meteorological Services of Angola. The publication by Silveira (1967) of recordings from 184 stations across all 18 provinces provides an invaluable record of the country's climate. According to the Ministry of Environment's Initial National Report to the UNFCCC (GoA 2013) the weather recording network collapsed from 225 'climatological posts' in 1974 to zero posts in 2010, while synoptic stations decreased from 29 in 1974 to 23 operational stations in 2010, 12 being automatic and 11 conventional. The network has since been strengthened by 22 automatic

Köppen symbol	Station	Altitude (m)	Precipitation (mm)	Mean of hottest month °C	Mean of coldest month °C
Aw	Belize	245	1612	26.7	22.2
Aw	Saurimo	1081	1355	23.8	20.3
Bsh	Ondgiva	1150	577	26.4	16.7
Bsh	Cuangar	1050	596	24.6	15.0
Bsh'	Chitado	1000	405	27.4	19.2
Bsh'	Luanda	44	405	27.0	20.1
Bwh	Moçâmedes	44	37	24.2	15.5
Bwh	Tômbwa	4	12	24.2	14.5
Bwh'	Benguela	7	184	26.3	18.0
Bwh'	Caraculo	440	123	26.4	17.2
Cwa	Menongue	1348	965	23.4	14.5
Cwa	Luena	1328	1182	22.7	17.0
Cwb	Huambo	1700	1210	20.6	15.7
Cwb	Lubango	1760	802	20.7	15.3

Table 2.1 Representative climatic data following the Köppen climate classification system

Data from Silveira (1967)

stations established by the Southern African Science Service Centre for Climate Change and Adaptive Land Management (SASSCAL).

The poor national coverage and reliability of climatic data collected over the past four decades is a challenge for climate change research. However, a recent study (Carvalho et al. 2017) provides the first analysis and comparison of a set of four Regional Climate Models (RCMs) with data from 12 meteorological monitoring stations in Angola. Scenarios of future temperature and precipitation anomaly trends and the frequency and intensity of droughts are presented for the twenty-first century. While there is a difference in the performance of the four RCMs, in particular for precipitation, consistent results were found for temperature projections, with an increase of up to 4.9 °C by 2100. The temperature increases are lowest for the northern coastal areas and highest for the southeast. In contrast to temperature rises, precipitation was projected to fall over the century, with an average of -2% across the country. Again, the strongest change was projected for the southeast, with decreases of up to -4%. Due principally to the projected increase in Sea Surface Temperatures by approximately 3 °C over the Atlantic during the twenty-first century, the central coastal region is expected to have a slight increase in precipitation.

Carvalho et al. (2017) highlight the extreme climate vulnerability of Angola, as previously noted by other studies (Brooks et al. 2005; Cain and Cain 2015). They conclude that climate change in Angola will bring stronger and more frequent droughts through the century, with impacts on water resources, agricultural productivity and wildfire potential. These factors will no doubt play out in negative ways on the current trends of land transformation and degradation as described by Mendelsohn (2019).

Biogeography, Biomes and Ecoregions

Overview

Angola's geographic location, geological history, climate and physiography account for its rich biological diversity. The comparative paucity of research focused on or within Angola explains the dependence of descriptions of the country's biogeography on broader regional reviews. While a full synthesis and interpretation of the evolution of the country's fauna and flora awaits development (Cotterill 2010, 2015), recent workers have advanced towards consensus on the main patterns, as discussed in general terms for terrestrial biota in this chapter, for marine systems by Kirkman and Nsingi (2019) and Weir (2019), and for freshwater fishes by Skelton (2019) in other chapters of this volume.

In brief, three marine ecoregions (Spalding et al. 2007) are within or overlap with Angola's marine environment, namely the Guinea South, Angolan, and Namib Ecoregions, the first two of which belong to the tropical Gulf of Guinea biogeographical province whereas the latter is part of the Benguela biogeographical province (Kirkman and Nsingi 2019). Most of Angola's EEZ falls within the Benguela Current Large Marine Ecosystem, with only Cabinda in the far north being included in the Guinea Current Large Marine Ecosystem.

The freshwater ecoregions of Africa have been classified and mapped by Thieme et al. (2005) and the eight ecoregions found within Angola are described in this volume (Skelton 2019). Skelton (2019) provides an elegant biogeographic model to explain the patterns and dynamics of freshwater fish faunas of Angola. Neither the floral nor vegetation patterns reflect the complexities and subtleties embedded in the ichthyological zoogeography of Angola, given the mobility of terrestrial plant dissemination. Here I will confine discussion to the terrestrial biota and ecosystems.

Angola lies between and within two major terrestrial biogeographic regions: the moist forests and savannas of the Congolian region; and the woodlands, savannas and floodplains of the Zambezian region. These two major divisions occupy over 97% of Angola. Gallery and escarpment forests of Congolian affinity penetrate southwards into the Zambezian savannas and woodlands of the Angolan *planalto* along deeply incised tributaries of the Congo Basin, and form a broken chain of forests southwards along the western escarpment. In the south, the extensive *Brachystegia/Julbernardia* miombo woodlands that occupy most of central Angola transition to *Baikiaea/Guibourtia/Burkea* savannas and woodlands. In the southwest, the arid *Acacia/Commiphora/Colophospermum* savannas, dwarf shrublands and desert of the Karoo-Namib region are found, penetrating northwards as a narrowing wedge along the coastal lowlands to Cabinda. The smallest of Africa's centres of botanical endemism – the *Podocarpus* Afromontane forests and montane grasslands – are represented by extremely restricted, relict patches in the mountains of the Benguela, Huambo and Huíla highlands.

Early Studies

Beyond general agreement on the above brief outline, botanists and zoologists have described and debated as many systems of biogeographic classification and of terminologies for Angola and for Africa as there are authors of the papers on the topic (Werger 1978). The pioneering works of Welwitsch (1859); Gossweiler and Mendonça (1939) and Barbosa (1970) provided the basis for several subsequent attempts to integrate the vegetation of Angola within a regional framework (Monteiro 1970; White 1971, 1983; Werger 1978). Zoogeographic classifications (Chapin 1932; Frade 1963; Monard 1937; Hellmich 1957; Crawford-Cabral 1983) are, with some minor exceptions, compatible with the overall systems of botanists (Werger 1978; Linder et al. 2012), (but see Branch et al. 2019, for comments on lizards). The Africa-wide synthesis of White (1983) is particularly useful in considering Angola's floristic (and in general terms, zoological) patterns and affinities. In broad terms, and following White's terminology, Angola includes representation of four 'regional centres of endemism'. They comprise the following centres with estimates of the percentage of their total area in Angola from Huntley (1974a, 2010):

- Guineo-congolian regional centre of endemism mosaics of forests, thickets, tall grass savannas 25.7% (This is Linder et al.'s Congolian Region and includes their Shaba sub-region);
- Zambezian regional centre of endemism moist woodlands, savannas, grasslands and thickets 71.6% (The Zambezian Region sensu Linder et al.);
- Karoo-Namib regional centre of endemism desert, shrublands, arid savannas, woodlands and thickets – 2.6% (Most of this is placed in Linder et al.'s Southern African Region as their Southwest Angola sub-region); and
- Afromontane archipelago-like regional centre of endemism forests, savannas and grasslands 0.1%. (This is related to Linder et al.'s Ethiopian Region).

Statistical Regionalisation

Attempts have recently been made to use the massive databases of species distribution records held by museums and herbaria to bring objectivity and consistency to the classification of Africa's floral and faunal regions. A major step towards such regionalisation is provided by the statistical definition of biogeographical regions of sub-Saharan Africa by Linder et al. (2012). Using data for 1877 grid cells of one-degree resolution, the study included data for over a million records of 1103 species of mammals, 1790 species of birds, 769 species of amphibians, 480 species of reptiles and 5881 species of vascular plants. The databases were analysed using cluster analysis techniques to define biogeographical units that "comprise grid cells that are more similar in species composition to each other than to any other grid cells" (Linder et al. 2012). They proposed seven biogeographical regions for sub-Saharan

Africa: Congolian, Zambezian, Southern African, Ethiopian, Somalian, Sudanian and Saharan. Their analyses demonstrated that patterns of richness and endemism are positively and significantly correlated among plants, mammals, amphibians, birds and reptiles and with the overall biogeographical regions revealed by the sum of the data sets.

The use of modern cluster analysis techniques was taken further, at an Angolan level, by Rodrigues et al. (2015). Based on a cluster analysis of data for 9880 records of 140 species of ungulates, rodents and carnivores at a quarter degree resolution, the study found general congruence with that of Linder et al. (2012) and the earlier divisions of Angola's biogeography (Beja et al. 2019). Rodrigues et al. (2015) identify 18 indicator species for their four main divisions, which agree with the groupings based on field surveys undertaken in the 1970s (Huntley 1973) that also included the enclave of Cabinda, which was not included in the Rodrigues et al. (2015) analyses.

Both of the above very detailed and objective cluster analyses confirmed the general patterns of biogeographical regionalisation used for many decades across Africa, as described at the head of this section, even though terminology and detail of boundaries and transitions between regions differ from one author to the next. While objective, it is possible that the cluster analysis approach lacks the subtlety and flexibility of scale that classical expert systems permit. A particular challenge is the paucity of geo-referenced data for Angolan taxa, as experienced in a recent botanical analysis at inter-tropical scale (Droissart et al. 2018). Both cluster analyses and expert systems remain works in progress.

Biomes and Ecoregions

The chorological studies of White (1983) and statistical analyses of Linder et al. (2012) capture some of the evolutionary history and relationships of Africa's flora and fauna, but they do not fully reflect the continent's diversity of biomes, habitats and ecosystems – which are based on structural and functional rather than evolutionary relationships. The most comprehensive recent synthesis on African habitats (Burgess et al. 2004) has been widely adopted as a basis for conservation planning and is of use for any study of African biomes, ecoregions and habitats (MacKinnon et al. 2016). At the first level, a global classification and map of the world's ecoregions (Olson et al. 2001) was used to identify the nine biomes of Africa's three main biogeographic divisions (Palearctic, Afrotropical and Cape). The biome concept used was defined as "vegetation types with similar characteristics grouped together as habitats, and the broadest global habitat categories are called biomes" (Olson et al. 2001). Of the nine biomes recognised, seven are represented in Angola – the largest range of biomes represented in any African country. These are:

- Tropical and subtropical moist forests;
- Montane grasslands and shrublands;

- Tropical and subtropical grasslands, savannas, shrublands, and woodlands;
- · Tropical and subtropical dry and broadleaf forests;
- · Deserts and xeric shrublands;
- · Mangroves; and
- · Flooded grasslands and savannas.

Within the biomes, Burgess et al. (2004) defined a total of 119 terrestrial ecoregions for Africa and its islands. Ecoregions are defined as "large units of land or water that contain a distinct assemblage of species, habitats and processes, and whose boundaries attempt to depict the original extent of natural communities before major land-use change" (Dinerstein et al. 1995). It is impressive to note that based on the Burgess et al. (2004) assessment, Angola has not only the largest diversity of biomes, but also the second largest representation of ecoregional diversity in Africa (Table 2.2, Fig. 2.8).

Figure 2.8 (Burgess et al. 2004) provides a useful framework for the understanding of Angola's biodiversity patterns. Despite its coarse grain, it allows a general synthesis to be refined as new information becomes available. The relationship between biomes and ecoregions (*sensu* Burgess et al. 2004) and the vegetation types of Barbosa (1970) is summarised in Table 2.3. The very brief notes on key genera found within the Barbosa vegetation units provide an idea of the floristic composition that characterises the ecoregion. The photos presented in Fig. 2.9 provide examples of the main vegetation types and habitats

The Biological Importance of the Angolan Escarpment

While the classification of White (1983) and Linder et al. (2012) are useful at a continental scale, a more detailed and subtle analysis of the major biomes and habitat groupings is needed at a national scale for both research and conservation

Country	Biomes	Ecoregions number and total (T)	
Angola	7	8, 32, 42, 43, 49, 50, 51,55, 56, 63, 81, 82, 106, 109, 116	15
Botswana	3	54, 57, 58, 63, 68, 105	6
Congo Republic	3	8, 12, 13, 43,116	5
D.R. Congo	5	8, 13, 14, 15, 16, 17, 42, 43, 49, 50, 73, 116	12
Mozambique	3	21, 22, 52, 53, 54, 64, 76, 117	8
Namibia	3	51, 55, 58, 67, 105, 106, 107, 108, 109, 110	10
South Africa	5	22, 23, 24, 54, 57, 58, 77, 78, 79, 80, 89, 90, 91, 105, 108, 110, 117	17
Zambia	4	32, 50, 53, 54, 56, 63, 74	7
Zimbabwe	2	51, 53, 54, 57, 58, 76	6

Table 2.2 Representation of biomes and ecoregions in southern African countries

From Burgess et al. (2004)

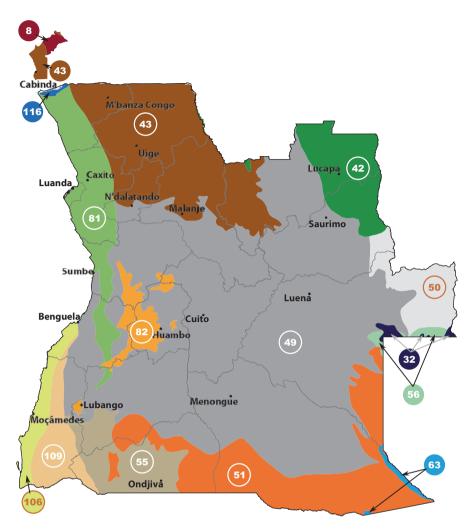


Fig. 2.8 Ecoregions of Angola

8 Atlantic Equatorial Coastal Forest • 32 Zambezian *Cryptosepalum* Dry Forest • 42 Southern Congolian Forest-Savanna Mosaic • 43 Western Congolian Forest-Savanna Mosaic • 49 Angolan Miombo Woodland • 50 Central Zambezian Miombo Woodland • 51 Zambezian *Baikiaea* Woodland • 55 Angola Mopane Woodland • 56 Western Zambezian Grassland • 63 Zambezian Flooded Grasslands • 81 Angolan Scarp Savanna and Woodland • 82 Angolan Montane Forest-Grassland Mosaic • 106 Kaokoveld Desert • 109 Namib Escarpment Woodlands • 116 Central African Mangroves. (After Burgess et al. 2004, map used with permission)

Table 2.3 African biomes and ecoregions (as defined by Burgess et al. 2004) and Angolan vegetation types (Barbosa 1970) with indicative genera

Ecoregion n°	Biome	Ecoregion	Barbosa n°, name and key genera
8	Tropical and Subtropical	Atlantic Equatorial	1,2. Closed Forest
0	Forest	Coastal Forest	Gilbertiodendron, Librevillea,
	rotest	Coustai i orest	Tetraberlinia
32	Tropical and Subtropical	Zambezian Cryptosepalum	4. Closed Forest
	Dry Broadleaf Forest	Dry Forest	Cryptosepalum, Brachystegia, Erythrophleum
42	Tropical and Subtropical	Southern Congolian	8. Forest-Savanna Mosaic
	Grasslands, Savannas, Shrublands and Woodlands	Forest-Savanna Mosaic	Marquesia, Berlinia, Daniella Hymenocardia
43	Tropical and Subtropical	Western Congolian	3. Closed Forest
	Grasslands, Savannas,		Celtis, Albizia, Celtis
	Shrublands and Woodlands	Forest-Savanna	13. Thicket-Forest Mosaic
		Mosaic	Annona, Piliostigma, Andropogon, Hyparrhenia
49	Tropical and Subtropical	Angolan Miombo	16, 17, 18. Woodland
	Grasslands, Savannas, Shrublands and Woodlands	Woodland	Brachystegia, Julbernardia, Guibourtia, Burkea, Pterocarpus
50	Tropical and Subtropical	Central Zambezian	17, 19. Woodland
	Grasslands, Savannas, Shrublands and Woodlands	Miombo Woodland	Brachystegia, Julbernardia, Cryptosepalum
51	Tropical and Subtropical	Zambezian Baikiaea	25. Tree and Shrub Savanna
	Grasslands, Savannas, Shrublands and Woodlands	Woodland	Baikiaea, Guibourtia, Pterocarpus, Combretum
55	Tropical and Subtropical	Angola Mopane	20. Woodland
	Grasslands, Savannas, Shrublands and Woodlands	Woodland	Colophospermum, Croton, Combretum, Sclerocarya, Acacia
56	Tropical and Subtropical	Western Zambezian	31. Grasslands
	Grasslands, Savannas, Shrublands and Woodlands	Grassland	Loudetia, Monocymbium, Tristachya, Parinari, Syzygium
63	Flooded Grasslands and	Zambezian Flooded	31. Grasslands
	Savannas	Grasslands	Loudetia, Echinochloa, Oryza
81	Montane Grasslands and Shrublands	Angolan Scarp Savanna and Woodland	10, 11, 22, 23. Forest- Savanna-Woodland-Thicket Mosaic
			Adansonia, Acacia, Albizia, Celtis, Piliostigma
82	Montane Grasslands and Shrublands	Angolan Montane Forest-Grassland	6, 32. Relict Forest, Grasslands
		Mosaic	Podocarpus, Apodytes, Pittosporum, Protea, Erica

(continued)

Table 2.3 (continued)

Ecoregion n°	Biome	Essesian	Barbosa n°, name and key
n ·	Biolile	Ecoregion	genera
106	Deserts and Xeric	Kaokoveld Desert	28, 29. Desert, Steppes
	Shrublands		Welwitschia, Zygophyllum,
			Stipagrostis, Odyssea
109	Deserts and Xeric	Namib Escarpment Woodlands	27. Steppes
	Shrublands		Acacia Commiphora,
			Colophospermum,
			Sesamothamnus, Rhigozum
116	Mangroves	Central African Mangroves	14 A. Mangroves
			Rhizophora, Avicennia,
			Raphia, Elaeis

planning in Angola (Revermann and Finckh 2019). What is equally important in biogeographic analysis is the detection of patterns of endemism and diversity at dispersed scales - such as the Angolan Escarpment Zone - described by Hall (1960a) and subsequently recognised by many workers as of great biodiversity and evolutionary importance (Huntley 1973, 1974a, 2017; Hawkins 1993; Mills 2010; Clark et al. 2011). Indeed, each taxon-based account in this volume, on plants (Goyder and Gonçalves 2019), odonata (Kipping et al. 2019), lepidoptera (Mendes et al. 2019), fishes (Skelton 2019), birds (Dean et al. 2019), amphibians (Baptista et al. 2019), reptiles (Branch et al. 2019) and mammals (Beja et al. 2019) draws attention to the importance of the Angolan Escarpment as a centre of endemism and speciation. Hall (1960a) explained her recognition of the importance of the Angolan Escarpment as the major speciation hotspot for birds in Angola by it: (i) creating a barrier between arid-adapted species of the coastal plains and of the miombo woodlands of the plateau, (ii) creating a steep ecological gradient, and (iii) functioning as a refuge for moist forest specialists that were isolated here during the dry periods of the glacial cycles. Dean et al. (2019) note that 75% of Angola's endemic birds are found in this zone.

The Angolan Escarpment and the remote, isolated and fragmentary remnants of Afro-montane forests of the Angolan Highlands offer ideal testing grounds for biogeographic models, as recently explored by Vaz da Silva (2015). The Angolan Escarpment biogeographic unit awaits clear definition, description and demarcation, but its scientific importance is matched only by the vulnerability of its threatened forest habitats (Cáceres et al. 2015). Linder et al. (2012) similarly recognise the importance of the Angolan Escarpment, and that of the transition from Congolian to Zambezian regions along the northern border of Angola (which they place in their Shaba sub-region). High species replacement values are found across these biologically rich areas, emphasising the urgency for their protection.

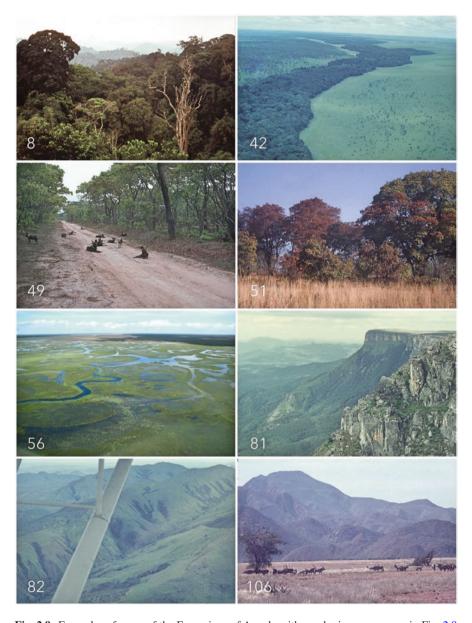


Fig. 2.9 Examples of some of the Ecoregions of Angola with numbering as per map in Fig. 2.8 and summary in Table 2.3. 8. Maiombo Forest, Cabinda; 42. Congolian gallery forest and moist miombo woodlands and savanna grasslands, Lunda-Norte; 49. *Brachystegia/Julbernardia* woodland Luando Strict Nature Reserve, Malange; 51. *Baikiaea/Guibourtia* Woodland Mucusso, Cuando Cubango; 56. Wetlands of the Bulozi Floodplain, Moxico; 81. Angolan Escarpment at Serra da Chela, Tundavala, Huíla; 82. Remnant patches of Afromontane forest in ravines on Mount Moco, Huambo; 106 Grasslands of the intermontane plains of central Iona National Park, Namibe. (Photos: Bulozi – JM Mendelsohn, others by BJ Huntley)

Conclusions

This brief outline of the biogeography of Angola demonstrates the country's unusual diversity of landscapes, climates and ecoregions, with Angola embracing the highest number of biomes represented within any African state.

The many classifications and terminologies applied to Angola's biogeographic units over the past century have not yet resulted in a nationally adopted nomenclature for its biomes and habitats. This situation prevails despite the existence of strong traditions in Angola's ethnic groups of indigenous taxonomies for habitats, such as those of the Chokwe of the Lundas, that are as perfect and detailed as modern systems (Redinha 1961; Huntley 2015). Furthermore, while many vernacular terms (mato de panda, anharas do alto, floresta cafeeira, muxitos, mulolas, chanas da borracha, etc.) enjoy wide use, they are imprecise and inadequate for Angola's great diversity of biomes and habitats.

The absence of a uniform system of nomenclature limits the use of information attached to biological collections, which in most cases provide only site locality data, and more recently, geo-referencing. Several southern African countries have nationally accepted biome and vegetation maps (e.g. South Africa, Lesotho and Swaziland – Mucina and Rutherford 2006) with clear descriptors for each biome and vegetation unit, facilitating communication between researchers and conservation planners. As Angola re-assesses its biodiversity wealth, and the need to protect and sustainably utilise these resources, the development of a new map of its vegetation, ecosystems and biomes becomes a high priority. Equally urgent but similarly daunting is the study of the evolutionary processes and relationships of the biota of the Angolan Escarpment and Afromontane forests, and the effective protection of these fingerprints of the past.

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