Monograph on

Endemism in the Highlands and Escarpments of Angola and Namibia



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Published with support and funding from:

Ongava Research Centre (ORC)
Namibian Chamber of Environment (NCE)
Centro de Investigação em Biodiversidade
e Recursos Genéticos (CIBIO)
B2Gold Namibia
Total Energies

Language editor: Carole Roberts
Design and layout: Alice Jarvis

NE Namibian Journal of Environment

2023: Volume 8 www.nje.org.na

ISSN: 2026-8327 (online)

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Biomes and ecoregions of the highlands and escarpments of Angola and Namibia

BJ Huntley

URL: https://www.nje.org.na/index.php/nje/article/view/volume8-huntley Published online: 15th December 2023

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ARSTRACT

This paper outlines the extraordinarily rich diversity of biomes and ecoregions found within the highlands and escarpments of Angola and Namibia (HEAN). Across 2,700 km of latitude, the climate ranges from tropical summer rainfall averaging at 1,200 mm per year in the north to warm temperate non-seasonal rainfall of 100 mm per year in the extreme southwest. Biomes range from Guinea-Congolian rainforests, Afromontane forests and grasslands, arid and mesic savannas and woodlands, to the Namib Desert. The concepts of biomes, ecoregions and endemism are discussed, and these terms applied to the four biomes and twelve ecoregions falling within the HEAN.

Keywords: Angola, biomes, ecoregions, escarpments, highlands, Namibia, vegetation types

INTRODUCTION

Across the 2,700 km latitudinal extent of the highlands and escarpments of Angola and Namibia (HEAN), from Cabinda to the Orange River, climates range from tropical summer rainfall in the north to warm temperate non-seasonal or mildly winter rainfall in the extreme southwest, and from 1,200 mm to 100 mm precipitation per year from north to south across this range (see Figures 8 and 9 in Mendelsohn & Huntley 2023). The physiographic diversity and steep precipitation gradient from north to south account for the extraordinary richness of biomes, ecoregions and vegetation types, and animal and plant species, found along this spine of landscapes that extends across western Angola and Namibia.

In northern Angola, Guineo-Congolian rainforests clothe the sea-facing hills and escarpments of Cabinda, Zaire, Uíge, Bengo and Cuanza-Norte provinces, with remnants or elements in Cuanza-Sul, Benguela, Huambo and Huíla, within a matrix of firetolerant tall grasslands and open woodlands. On the highest peaks of Cuanza-Sul, Benguela, Huambo and Namibe provinces, isolated patches or elements of Afromontane forests survive in fire-protected mountain valleys, surrounded by short grasslands and open miombo Brachystegia woodlands. Mendelsohn and Gomes (2023: Figure 2) for a map of provinces. Southwards, Acacia, Commiphora, Colophospermum and Combretum woodlands and shrublands occupy the arid plains, hills and mountains of Namibe and Cunene provinces. The savanna floras of Angola are dominated by Zambezian taxa. The arid ecoregions of southern Angola continue across the highland plateaus, escarpments and inselbergs of Namibia. Increasing proportions of Nama Karoo plant affinities appear in the shrublands of southern Namibia. The northern outliers of the Succulent Karoo biome of South Africa appear on the hills surrounding the Orange River valley and southern coastal plains of the Pro-Namib.

BIOMES, ECOREGIONS AND ENDEMISM: CLASSIFICATION AND NOMENCLATURE

The classification and mapping of the biomes and ecoregions of Africa received much attention in the decades following the establishment of the Convention on Biological Diversity (CBD) in 1992, specifically in efforts to design and implement biodiversity conservation strategies and programmes. Preceding the CBD, White (1983) provided a useful 'big picture' framework of African vegetation and floristic relations within his phytochoria, without referencing these to biomes or ecoregions. Influenced by this pioneering work and following wide consultation, WWF-US led the preparation of a series of classifications and maps that serve as templates for studies at global, regional and national levels (Olson et al. 2001, Olson & Dinerstein 2002, Burgess et al. 2004). For the purposes of this outline, the global ecoregions map and its nomenclature (Dinerstein et al. 2017) is used and is applied here referencing the more recent syntheses of the Atlas of Namibia Team (2022) for Namibia, and Huntley (2023) for Angola.

While the highlands and escarpments include representatives of four African biomes and 12 ecoregions (*sensu* Dinerstein *et al.* 2017), biological and ecological conditions in the physiographically diverse highland system often differ from those in the broader, more generalised biomes and ecoregions of southern Africa of which they form part. Thus many endemics reported from within the HEAN occur in specialised habitats, such as rock outcrops, wetlands,

the spray zone of waterfalls or isolated forest fragments. An endemic is defined here as a species that only occurs in the area of concern (e.g., HEAN, Angolan Planalto, Khomas Hochland). Near-endemics are species with a limited distribution outside the core area which defines the endemic. A centre of endemism is an area in which restricted-range species overlap, or a localised area which has a high occurrence of endemics. Within the HEAN, areas with appreciable levels of endemism are mostly subsets of wider centres of which they are relatively depauperate outliers, such as the isolated fragments of the Afromontane archipelago-like regional centre of endemism of White (1983) which occur in the Angolan highlands.

The biome concept has become widely applied in the ecological and biodiversity literature, and has been

comprehensively reviewed by Mucina (2019). Although increasingly understood as the largest category of structurally and functionally similar habitats and their biota which share climate, soil and disturbance factors, the use of the term 'biome' varies widely between authors. In relation to the HEAN, three different applications are worth noting. The HEAN area includes four biomes and 12 ecoregions as defined by Dinerstein et al. (2017). However, the Atlas of Namibia Team (2022) includes four biomes (Treeand-Shrub Savanna, Nama Karoo, Succulent Karoo and Namib Desert) within the single 'Deserts and Xeric Shrublands Biome' of Dinerstein et al. (2017). Huntley (2023) distinguishes between Arid and Mesic Savanna biomes, which fall within the Tropical and Subtropical Grasslands, Savannas and Shrublands Biome of Dinerstein et al. (2017) (Table 1).

Table 1: Biomes, ecoregions and vegetation types represented in the highlands and escarpments of Angola and Namibia (HEAN). Classifications and terms follow Dinerstein et al. (2017), Huntley (2023) and Atlas of Namibia Team (2022). Ecoregion numbers in the first column refer to numbered ecoregions in Figure 3 and accompanying text.

Global biome and ecoregion number and name (Dinerstein et al. 2017)	Angolan biome and ecoregion number and name (Huntley 2023)	Namibian biome and vegetation type number and name (Atlas of Namibia Team 2022)
Tropical and Subtropical Moist Broadleaf Forests/Tropical and Subtropical Grasslands, Savannas and Shrublands Biome	Guineo-Congolian Rain Forest Biome and Forest/Savanna Mosaics	(Not represented)
5. Congolian Coastal Forest	1. Congolian Rain Forest	
63. Western Congolian Forest–Savanna	2. Western Congolian Forest/Savanna Mosaic	
Montane Grasslands and Shrublands Biome	Afromontane Forest and Grassland Biome	(Not represented)
77. Angolan Montane Forest– Grasslands	4. Afromontane Forest5. Montane Grassland	
Tropical and Subtropical Grasslands, Savannas and Shrublands Biome	Mesic Savanna Biome	Tree-and-Shrub Savanna Biome
35. Angolan Scarp Savanna and Woodlands	6. Angolan Escarpment Savannas	
36. Angolan Wet Miombo Woodlands	7. Angolan Wet Miombo Woodlands	
	Arid Savanna Biome	
34. Angolan Mopane Woodlands	12. Angolan Mopane Woodlands	20. Western Highlands16. Karstveld
Deserts and Xeric Shrublands Biome		
104. Namibian Savanna Woodlands	13. Namib Savanna Woodlands	
		Nama Karoo Biome
		Central-Western Escarpment and Inselbergs Desert – Dwarf Shrub Transition Northwestern Escarpment and Inselbergs
97. Kalahari Xeric Savanna		19. Thornbush Shrubland 15. Highland Shrubland
94. Gariep Karoo		8. Dwarf Shrub Savanna 11. Karas Dwarf Shrubland
100 M		Succulent Karoo Biome
102. Namaqualand–Richtersveld Steppe	Namib Desert Biome	4. Succulent Steppe Namib Desert Biome
98. Kaokoveld Desert	15. Angolan Namib Desert	1. Northern Desert
103. Namib Desert	13. Aligoran Namio Desert	
103. Namio Desert		2. Central Desert3. Southern Desert

Greater consensus is found regarding the ecoregions of the HEAN. An ecoregion is defined by Dinerstein *et al.* (1995) as: "A large unit of land or water that contains 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." The varied application of the biome concept and constituent ecoregions within the HEAN, and their nomenclature, is summarised in Table 1.

The vegetation types of Angola and Namibia were mapped and described respectively by Barbosa (1970) and Giess (1971) using their extended field experience and expert knowledge of the flora, in addition to drawing on earlier studies. These early studies are summarised by Revermann and Finckh (2019) for Angola and Westinga et al. (2020) for Namibia. Given the succession of maps, interpretation of patterns, and use of terms, their integration is not simple. Indeed, as the multiple maps of Namibia's vegetation presented by Westinga et al. (2020) demonstrate (Figure 1), the student might have difficulty in 'seeing the wood for the trees'. If one adds the phytochoria of White (1983) and natural floristic groups of Craven (2009) and Craven and Kolberg (2023) one can visualise a succession of the past (phytochoria, floristic groups) and present (vegetation types, green vegetation

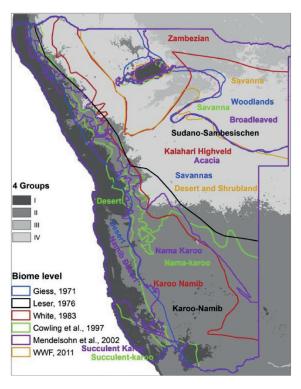


Figure 1: A compilation of the six published biome level maps of Namibia and NDVI-profile cluster-groups (shades of grey) of Westinga et al. (2020). The names given to each unit are those of the authors of the maps. Reproduced from Westinga et al. (2020).

biomass); a palimpsest of changing concepts and patterns over time. Such inconsistencies reflect the rapidly evolving and expanding biodiversity studies in the region.

BIOMES AND ECOREGIONS REPRESENTED IN THE HEAN

Within the constraints of successive vegetation maps, ecoregion delineations and biome definitions, the following outlines of the biomes (Figure 2) and ecoregions (Figure 3) within the HEAN provide a general background to the taxon-focused chapters of this monograph. The ecoregion numbers and nomenclature follow Dinerstein et al. (2017), while the vegetation type numbers of Barbosa (1970), Giess (1971), Atlas of Namibia Team (2022) and Huntley (2023), and the landscape unit numbers used in Mendelsohn and Huntley (2023: Figure 5) are added for ease of cross-referencing. For each of the biomes represented within the HEAN, the ecoregions it encompasses are described and illustrated, and a selected listing of vertebrate species typical of the broader biome - within Angola, and over much of Namibia – is given to help characterise the biome.

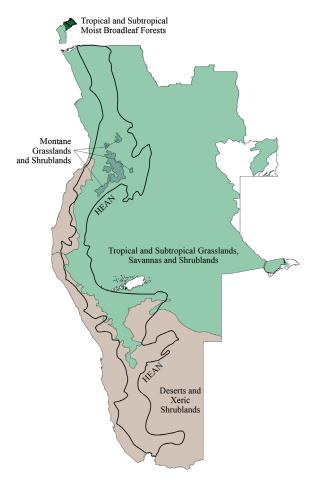


Figure 2: Biomes (Dinerstein et al. 2017) of the highlands and escarpments of Angola and Namibia (HEAN).

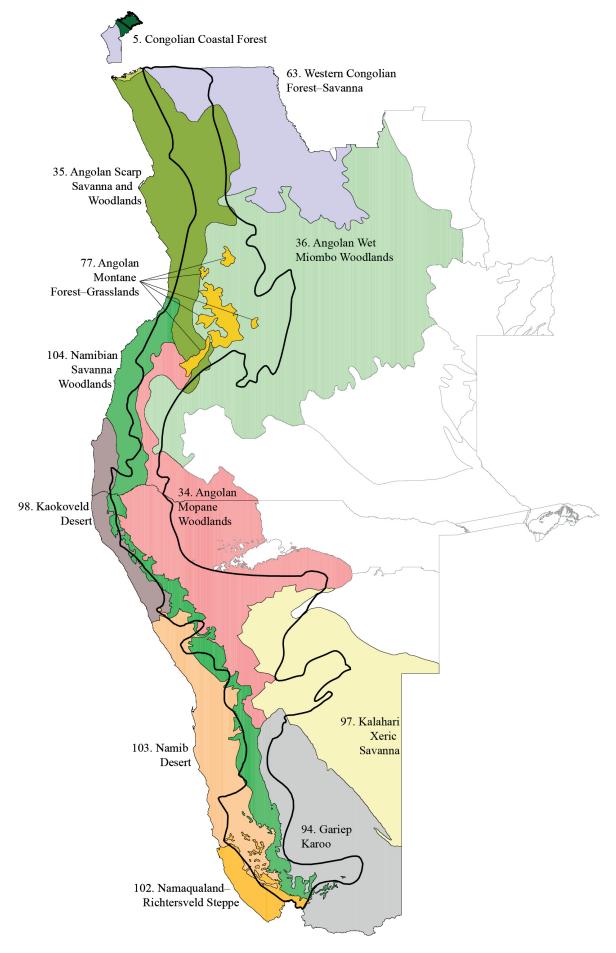


Figure 3: Ecoregions (Dinerstein et al. 2017) of the highlands and escarpments of Angola and Namibia (HEAN).

Tropical and Subtropical Moist Broadleaf Forests Biome

Across northern Angola, the rich Guineo-Congolian flora and fauna of African rainforests are represented in the moist forests found along the low mountains (400–1,200 masl) and escarpments of Cabinda, Zaire, Uíge, Cuanza-Norte, Cuanza-Sul and Malanje provinces. The biome comprises two ecoregions within the HEAN, Congolian Coastal Forest (5) and Western Congolian Forest–Savanna (63). Table 2 provides a synopsis of vertebrate species found within these forests, reflecting the species richness, in particular, of the remaining forests of Cabinda.

Ecoregion 5. Congolian Coastal Forest (Barbosa 1–3; Huntley 1; Landscape Unit 1).

These forests occur most extensively in Cabinda (Figures 4 and 5), where a continuation of the narrow belt of Lower Guinean evergreen to semi-evergreen broadleaf forest extends from central Cameroon to just north of the mouth of the Congo River. Outliers of Guineo-Congolian rainforest floristic and faunistic elements follow the Angolan escarpment in isolated blocks in Cuanza-Sul, and as tiny forest fragments in the seaward-facing ravines of the Chela Escarpment. The Alto Mayombe forests of Cabinda receive 1,200-1,400 mm of rain per annum, with fog a regular phenomenon. The canopy of mature forest in Mayombe may reach 50 m in height, but generally the canopy is 30-40 m in height. Important genera Gilbertiodendron, Julbernardia, Tetraberlinia in climax forest and Milicia, Musanga, Piptadeniastrum, Ricinodendron and Terminalia in disturbed, secondary forest. These forests are of great conservation importance (see Vaz Pinto et al. 2023).



Figure 4: Ecoregion 5. Congolian Coastal Forest. A subsistence farm in Alto Mayombe Forest, Cabinda. Tall trees include forest margin pioneer Terminalia superba with erect white trunks, and the branched crowns of Musanga cecropioides at left and right of the scene. Photo: Brian Huntley.

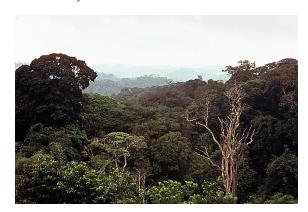


Figure 5: Ecoregion 5. Congolian Coastal Forest. Forest canopy, Alto Mayombe, Cabinda. Photo: Brian Huntley.

Table 2: Vertebrate species typical of the Guineo-Congolian rainforests of Angola, including those areas of Ecoregions 5 and 63 falling within the highlands and escarpments of Angola.

Amphibians	Congolese clawed frog, large-spotted reed frog, Benito river reed frog, Vilhena's reed frog, Carqueja's squeaker, Lameer's squeaker, Gabon forest tree frog
Reptiles	western forest feylinia, Owen's chameleon, variable bush viper, Gabon adder, forest night adder, Jameson's mamba, ringed water cobra, emerald snake, yellow-throated bold-eyed tree snake, forest twig snake
Birds	black guineafowl, afep pigeon, grey parrot, red-fronted parrot, great blue turaco, Guinea turaco, black bee- eater, African pied hornbill, black-and-white-casqued hornbill, piping hornbill, red-rumped tinkerbird, yellow-crested woodpecker, grey-green bushshrike, Angola white-throated greenbul, red-tailed loveleaf, banded prinia, forest chestnut-winged starling, dusky-blue flycatcher, Bannerman's sunbird
Mammals	African golden cat, Ansorge's cusimanse, African palm civet, bay duiker, white-bellied duiker, black-fronted duiker, sitatunga, red river hog, water chevrotain, white-belled (tree) pangolin, red-tailed monkey, moustached monkey, blue monkey, black-footed crowned monkey, De Brazza's monkey, putty-nosed monkey, Angola colobus, black-crested mangabey, northern talapoin, southern talapoin, Demidoff's dwarf galago, Thomas's dwarf galago, western lowland gorilla, central chimpanzee, golden potto, Milne-Edwards's potto, forest elephant, Beecroft's scaly-tailed squirrel

Ecoregion 63. Western Congolian Forest–Savanna (Barbosa 7–10; Huntley 2; Landscape Unit 2).

A large block of mixed forest and tallgrass savanna extends the reach of rainforests as gallery forests in valleys, and isolated forest fragments on hillsides and plateaus, southwards from the Congo Basin (Figure 6). The landscapes range 800-1,500 masl in the mountainous regions of Zaire and Uíge provinces (Lautenschläger et al. 2023). Precipitation of 1,000-1,400 mm falls per annum with fog being an important factor. Forest covers less than 5% of this mosaic, including species of Entandrophragma, Milicia, Musanga, Piptadeniastrum, Raphia and *Xylopia*. Trees of the fire-prone tallgrass savannas include genera such as Annona, Erythrophleum, Hymenocardia, Piliostigma and Strychnos, mesic woodlands include Brachystegia, Julbernardia, Burkea and Isoberlinia and drier woodlands include Dialium, Daniellia, Cryptosepalum and Marquesia.



Figure 6: Ecoregion 63. Western Congolian Forest–Savanna. This forest and savanna mosaic is near Camabatela, Cuanza-Norte. Tall grasses of Hyparrhenia and Trachypogon species, with a fire-tolerant Hymenocardia acida in left foreground. Photo: Brian Huntley.

Montane Grasslands and Shrublands Biome

Angola's most isolated and vulnerable biome comprises forests and grasslands of White's (1983) archipelago-like regional centre of endemism. The highest areas of the Angolan plateau and mountains have small areas of montane grassland on the Cuanza-Sul, Huambo, Huíla, Benguela and Bié highlands, much of it forming the Angolan Planalto. Very small remnants of Afromontane flora survive in the forests and shrublands along the Marginal Mountain Chain - specifically on Serra do Môco, Mount Namba and in ravines of the Chela Escarpment and the Humpata Plateau. They are important areas of biotic richness and endemism, although they occupy only 1.1% of Angola. Afromontane forests and grasslands are absent from Namibia. Vertebrate species typical of the Afromontane forests and grasslands of Angola are listed in Table 3.

Ecoregion 77. Angolan Montane Forest—Grasslands (Barbosa 6, 32; Huntley 4, 5; Landscape Units 3, 5).

The Afromontane forests of Angola are the most fragmented and isolated of all representatives of the Afromontane centre of floristic endemism in Africa, being over 2,000 km from related forests in Cameroon, South Africa and East Africa. With a total area of less than 1,000 ha across their entire range in Angola, they occur as small forest patches that are provided some shelter from fire in deep valleys and by rock outcrops (Powell et al. 2023). These highland sites receive between 800 and 1.600 mm of rainfall per annum, lying at 1,800-2,400 m elevation. The weakly stratified forests have a broken canopy of up to 20 m in height. Trees include Afromontane genera such as Apodytes, Cassipourea, Erythroxylum, Halleria, Ilex, Maesa, Myrica, Nuxia, Pittosporum and Podocarpus (Figures 7 and 8). The montane grasslands of the Angolan Marginal Mountain Chain and Angolan Planalto extend across the highlands of Cuanza-Sul, Benguela, Huambo, Bié and Huíla (Figures 9-11). Lying mostly between 1,500 and 1,800 masl, the rolling hills rise to 2,620 masl on

Table 3: Vertebrate species typical of the Afromontane forests and grasslands of Angola, including those areas of Ecoregion 77 falling within the highlands and escarpments of Angola.

Amphibians	Chela mountain reed frog, Anchieta's tree frog, Udzungwa ridged frog	
Reptiles	Benguela gecko, mountain day gecko, Angolan rough-scaled lizard, Marx's rough-scaled lizard, Angolan girdled lizard, Anchieta's chameleon, Angolan adder, link-marked sand racer	
Birds	Finsch's francolin, Swierstra's francolin, Ruwenzori nightjar, Fernando Po swift, naked-faced barbet, Margaret's batis, Perrin's bushshrike, Angola lark, black-collared bulbul, Brazza's martin, black-and-rufous swallow, Laura's woodland warbler, Huambo cisticola, Salvadori's eremomela, orange ground thrush, Angola slaty flycatcher, Bocage's sunbird, Ludwig's double-collared sunbird, Oustalet's sunbird, bronzy sunbird, black-chinned weaver, dusky twinspot, Angola swee waxbill, Fulleborn's longclaw, black-faced canary, thick-billed seedeater	
Mammals	common duiker	

Serra do Môco, the highest point in Angola. In many areas, seasonally waterlogged soils result in the near absence of trees but an abundance of grass, forb, geophyte and geoxyle species, including many orchids. (See Goyder *et al.* 2023 and Meller *et al.* 2023).

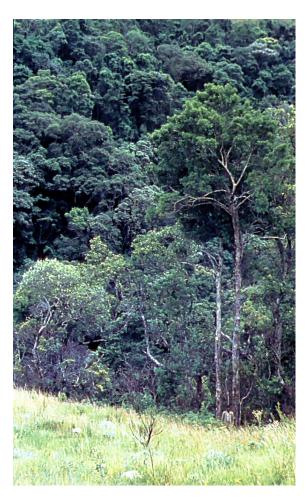


Figure 7: Ecoregion 77. Angolan Montane Forest-Grasslands. Fire-cut margin of Afromontane Forest on Serra do Môco, with Podocarpus milanjianus of 25 m height. Note the person standing at the base of the Podocarpus, for scale. Photo taken in 1972. Photo: Brian Huntley.



Figure 8: Ecoregion 77. Angolan Montane Forest–Grasslands. Isolated patch of Afromontane forest near Caluquembe, Huíla Province. Photo: Pedro Vaz Pinto.



Figure 9: Ecoregion 77. Angolan Montane Forest—Grasslands. Aloe grata on the slopes of Serra do Môco, overlooking montane grasslands of the Huambo highlands. Photo: Brian Huntley.



Figure 10: Ecoregion 77. Angolan Montane Forest-Grasslands. Fire-resilient Protea and Philippia shrubs scattered through short grassland on the summit of Serra do Môco, Huambo Province. Photo: Brian Huntley.



Figure 11: Ecoregion 77. Angolan Montane Forest–Grasslands. Moist montane short grassland at 2,000 masl, Humpata, Huíla Province. Photo: Brian Huntley.

Tropical and Subtropical Grasslands, Savannas and Shrublands Biome

The Zambezian flora of this biome dominates the highlands of Angola and Namibia, occupying over 90% of the HEAN in Angola and 37% in Namibia. Huntley (1982, 2023) and Owen-Smith (2021) have emphasised the distinction between the mesic-dystrophic and arid-eutrophic savannas of Africa, the structural and functional distinctions of which are highly relevant to the savanna ecoregions of the HEAN that extend from the moist equatorial forests of Cabinda to the hyperarid Namib Desert.

The mesic-dystrophic savannas, typical of the Zambezian centre of endemism, occupy over 80% of Angola, predominantly on the interior plateau, above 1,000 masl, and on freely draining nutrient-poor and acidic (dystrophic) soils. Fire is the key driving force that maintains the mix of grasses and trees that constitute the woodlands, savannas, shrublands and grasslands of mesic savannas. Although mesic savannas - including the Broadleaved Tree-and-Shrub Savannas of the Atlas of Namibia Team (2022) - occupy much of northwest Namibia, they do not extend into the HEAN other than on the Waterberg Plateau, a sandstone inselberg that rises above the surrounding arid acacia savannas. Vertebrates typical of the miombo woodlands of Angola, and mesicdystrophic savannas of central Africa, are listed in Table 4.

Arid-eutropic savannas cover 13% of Angola and 61% of Namibia where they are termed Acacia Tree-and-Shrub Savanna (Atlas of Namibia Team 2022). These savannas and shrublands are characterised by low rainfall (less than 650 mm per annum) and generally occur on richer (eutrophic) soils than the leached, nutrient-poor (dystrophic) Ferralsols and Arenosols of the mesic savannas of central Africa. Arid savannas skirt the HEAN, typically along the base of escarpments and inselbergs and river valleys, but reaching 2,000 masl on the summits of the arid mountains of Iona National Park in southwest Angola and the mountains of Namibia. Vertebrates typical of the arid-eutrophic savannas of Angola (and parts of Namibia) are listed in Table 5.

Ecoregion 35. Angolan Scarp Savanna and Woodlands (Barbosa 15, 18a, 22; Huntley 6; Landscape Units 2, 3).

South of the Congo River and along Angola's Central Escarpment, this narrow band of mixed savannas lies between the arid savannas of the coastal lowlands and miombo savannas of the high plateaus. A mosaic of tall grasslands and woodlands constitutes the Angolan Scarp Savanna and Woodlands. Trees include species of *Brachystegia*, *Burkea*, *Cochlospermum*, *Combretum*, *Cussonia*, *Pterocarpus*, *Terminalia* and *Uapaca*. Grasses are mostly species of the Andropogoneae (Figure 12).

Table 4: Vertebrate species typical of Angolan miombo woodlands, savannas and grasslands, including those areas of Ecoregions 35 and 36 falling within the highlands and escarpments of Angola.

Amphibians	Peter's clawed frog, Merten's striped toad, banded rubber frog, Guinea snout-burrower, Angolan reed frog, Benguela long reed frog, Senegal kassina, Bocage's burrowing tree frog, Angola ornate frog, sharp-nosed grass frog	
Reptiles	African dwarf mud turtle, Queen Nzinga's gecko, Iven's skink, Bayão's skink, Angola tree agama, Anchieta's cobra, spotted boomslang	
Birds	pale-billed hornbill, miombo barbet, western black-headed batis, Souza's shrike, miombo tit, red-capped crombec, short-winged cisticola, miombo wren warbler, black-necked eremomela, yellow-bellied hyliota, sharp-tailed starling, white-winged babbling starling, miombo scrub robin, Congo moor chat, Anchieta's sunbird, chestnut-backed sparrow-weaver, Bocage's weaver, bar-winged weaver	
Mammals	side-striped jackal, spotted hyaena, miombo genet, common duiker, greater galago	

Table 5: Vertebrate species typical of the arid savannas of Angola and Namibia, including those areas of Ecoregions 34, 97 and 104 (of the Deserts and Xeric Shrublands Biome), within the highlands and escarpments of the two countries.

Amphibians	Dombe toad, Grandison's pygmy toad, marbled rubber frog, African bullfrog
Reptiles	leopard tortoise, Ansorge's leaf-toed gecko, Angola banded thick-toed gecko, Huntley's sand lizard, Sundevall's writhing skink, horned adder, western banded spitting-cobra
Birds	ostrich, secretary bird, Monteiro's hornbill, white-tailed shrike, Benguela long-billed lark, rockrunner, Benguela long-tailed starling, rufous-tailed palm thrush, Cinderella waxbill
Mammals	black-backed jackal, bat-eared fox, Cape fox, cheetah, caracal, lion, leopard, spotted hyaena, brown hyaena, aardwolf, black-faced impala, springbok, Kirk's dik-dik, klipspringer, gemsbok, steenbok, greater kudu, plains zebra, Hartmann's mountain zebra

Ecoregion 36. Angolan Wet Miombo Woodlands (Barbosa 16–19; Huntley 7; Landscape Unit 4).

These woodlands, savannas and grasslands typically receive more than 1,000 mm of rainfall per year and lie at elevations of 900-1,500 masl. The deep, moist, dystrophic soils support a woodland canopy height of 15-25 m. Brachystegia spiciformis occurs in varying densities and robustness throughout the Angolan other Brachystegia species. miombo, with Julbernardia paniculata is also widespread across the miombo, together with Burkea, Cryptosepalum, Guibourtia and Pterocarpus species (Figures 13 and 14). On the edges of drainage-line grasslands (mulolas, dambos) species of Monotes, Protea and Uapaca occur as short trees. Grasses include species of Andropogon, Digitaria, Elionurus, Eragrostis, Hyparrhenia, Loudetia, Monocymbium and Setaria, with Panicum becoming prominent under woodland.

Ecoregion 34. Angolan Mopane Woodlands (Barbosa 20, 21, 27; Huntley 12; Giess 5; Atlas of Namibia Team 20, 21; Landscape Units 6–8).

The leguminous tree *Colophospermum mopane* occurs across the interior of the southern coastal lowlands and lower Cunene valley in Angola and extends southwards across the Western Highlands and Karstveld of Namibia, as the dominant species of woodlands, savannas and shrublands (Figures 15 and 16). *Colophospermum mopane* is typically found on heavy soils and stony hills receiving less than



Figure 12: Ecoregion 35. Angolan Scarp Savanna and Woodlands. Fire-tolerant Cochlospermum angolense trees are typical of the tall grasslands covering the rolling hills of this ecoregion. Photo: Brian Huntley.



Figure 13: Ecoregion 36. Angolan Wet Miombo Woodlands. Typical wet miombo in the Quibala hills, Cuanza-Sul Province. Photo: António Martins.

650 mm rainfall per annum and mostly below 1,000 masl in Angola and 1,200 masl in Namibia, but occurs at higher elevations on inselbergs and escarpment mountains. Although often found as a single dominant species in woodlands, *C. mopane* also forms mixed communities with species of *Adansonia*, *Albizia*, *Boscia*, *Combretum*, *Commiphora*, *Sclerocarya*, *Senegalia*, *Terminalia* and *Vachellia*.



Figure 14: Ecoregion 36. Angolan Wet Miombo Woodlands. Typical mature open miombo woodland of Brachystegia and Julbernardia, near Serra Mocoti. Note the continuous cover below the woodland canopy. Photo: John Mendelsohn.



Figure 15: Ecoregion 34. Angolan Mopane Woodlands. Mixed mopane woodlands and thicket below granite domes and inselbergs of the Angolan escarpment, between Lubango and Caraculo. Photo: Brian Huntley.



Figure 16: Ecoregion 34. Angolan Mopane Woodlands. Open mopane woodland in the foreground with karstveld hills in the background, all flushed green after recent rain. Commiphora, Combretum, Kirkia and Steganotaenia species dominate the karstveld woodland. Photo: John Mendelsohn.

Deserts and Xeric Shrublands Biome

Six of the ecoregions of the Deserts and Xeric Shrublands Biome as defined by Dinerstein et al. (2017) are represented in the HEAN (Table 1). These are Namibian Savanna Woodlands, Kalahari Xeric Savanna, Kaokoveld Desert, Namib Desert, Gariep Karoo and Namaqualand-Richtersveld Steppe. As noted above, this mix of arid ecoregions has been classified variously and differently by African biologists, especially those working in Angola, Namibia and South Africa. Mucina and Rutherford (2006) recognise, inter alia, Savanna, Nama Karoo, Succulent Karoo, and Desert biomes, each of which is represented in the single Deserts and Xeric Shrubland Biome of Dinerstein et al. (2017). Huntley (2023) places the Namibian Savanna Woodlands in his Arid Savanna Biome, while the Atlas of Namibia Team (2022) recognise a Nama Karoo Biome and a Succulent Karoo Biome, which are both represented within the Deserts and Xeric Shrublands Biome of Dinerstein et al. (2017) and which partially fall within the HEAN. The diversity of interpretations of the biome concept can hardly be more explicitly demonstrated. At a lower hierarchical level, the ecoregion concept is nevertheless useful. Vertebrate species typical of the Namibian Savanna Woodlands are listed in Table 5, and those of the Namib Desert are listed in Table 6.



Figure 17: Ecoregion 104. Namibian Savanna Woodlands. Namibian Savanna Woodlands dominated by Acacia species on the Talamajamba plateau, 40 km inland of Benguela. Rich grasslands are present following summer rain. Photo: António Martins.



Figure 18: Ecoregion 104. Namibian Savanna Woodlands. Mixed woodlands south of Serra da Neve, which rises to 2,489 masl. The dark green line of tall trees in the middle distance marks the Bentiaba River. Photo: Brian Huntley.

Table 6: Vertebrate species typical of the Namib Desert, including those areas of Ecoregions 98 and 103 falling within the highlands and escarpments of Angola and Namibia.

Reptiles	feathered-tailed gecko, Namib web- footed gecko, common Namib day gecko, Anchieta's dune lizard, Kaokoveld girdled lizard, desert plated lizard, speckled sand skink, dotted blind dart skink, Namaqua chameleon, Namib rock agama, Anchieta's dwarf python, Peringuey's adder, western sand snake
Birds	lappet-faced vulture, Ludwig's bustard, Rüppell's korhaan, Burchell's courser, Gray's lark, tractrac chat
Mammals	bat-eared fox, meerkat, brown hyaena, aardwolf, springbok, Kirk's dik-dik, gemsbok, Hartmann's mountain zebra

Ecoregion 104. Namibian Savanna Woodlands (Barbosa 27; Huntley 13; Giess 5; Atlas of Namibia Team 6, 7, 12; Landscape Units 3, 6, 8–10).

This ecoregion occupies a narrow belt of coastal lowlands and escarpment foothills and inselbergs which extend across 2,000 km from Sumbe in the north to the proximity of the Orange River in the south, as woodlands, scrubland and thickets wedged between the Namib Desert to the west and the Angolan Mopane Woodlands and Gariep Karoo ecoregions to the east. The landscapes include a mix of gravel and sandy plains, rolling stony hills and arid escarpments, mostly between sea level and 1,000 masl, but rising to 2,000 masl on Serra Cafema in Iona National Park, Angola, and in the Baynes and Gamsberg Mountains of Namibia. Rainfall decreases from north to south, from an annual average of 400 mm to 100 mm. Low trees and shrubs of the genera Acacia, Balanites, Boscia, Catophractes, Combretum, Commiphora, Euphorbia, Maerua, Rhigozum, Sesamothamnus, Sterculia and Terminalia form open savannas and shrublands (Figures 17–19).



Figure 19: Ecoregion 104. Namibian Savanna Woodlands. Open savanna and shrublands in the Hakos Mountains north of the Gamsberg with their sparse cover of Acacia, Boscia, Catophractes, Commiphora and other small trees and shrubs. Tribulus flowers adorn the foreground. Photo: John Mendelsohn.



Figure 20: Ecoregion 97. Kalahari Xeric Savanna. The Auas Mountains just south of Windhoek are dominated by grass cover in between scattered shrubs and small trees. Moltkeblick is the highest peak in the area and the second highest point in Namibia, rising to 2,479 masl. Photo: John Mendelsohn.



Figure 21: Ecoregion 97. Kalahari Xeric Savanna. Dense Acacia and Dichrostachys bush cover much of the Central-Western Plains landscape. Photo: John Mendelsohn.



Figure 22: Ecoregion 94. Gariep Karoo. Open grassland and scattered small shrubs characterise much of the Gariep Karoo in Namibia. Photo: Peter Cunningham.



Figure 23: Ecoregion 102. Namaqualand–Richtersveld Steppe. There is a great variety of succulents in the hills of the Aurusberge. Photo: John Pallett.

Ecoregion 97. Kalahari Xeric Savanna (Giess 7, 8; Atlas of Namibia Team 15, 19; Landscape Units 8, 9). The deciduous woodlands and shrublands of the Kalahari extend westwards to the central highlands of Namibia, including the Khomas Hochland, which lies at 1,700–2,000 masl. The highlands comprise rolling hills covered by shrubs and low trees (Figure 20), with species of Acacia, Boscia, Combretum, Euclea, Searsia, Tarchonanthus and Ziziphus being prominent. To the east, the elevation drops and the plateau is covered by deep Kalahari sands and open tree savannas and grasslands (Figure 21).

Ecoregion 94. Gariep Karoo (Giess 9; Atlas of Namibia Team 8, 11; Landscape Unit 10).

The Gariep Karoo is a northwestern extension of the vast Nama Karoo Biome of low shrublands that covers more than a third of South Africa's arid interior plateau. The Nama Karoo Basin of southeast Namibia is a large, flat plateau at 900–1,400 masl, underlain by sedimentary rocks and covered by dwarf shrubs, sparse grasses and scattered short trees (Figure 22). Shrubs include species of Aizoon, Eriocephalus, Pentzia, Pteronia and Salsola. Low trees and shrubs include species of Acacia, Boscia, Catophractes, Euclea, Rhigozum, Searsia and Tamarix.

Ecoregion 102. Namaqualand–Richtersveld Steppe (Giess 4, Atlas of Namibia Team 4; Landscape Unit 11).

This ecoregion represents a northern outlier of the Succulent Karoo Biome of South Africa. The primary ecological feature of this ecoregion, distinct from all others in the HEAN, is the weakly seasonal winter rainfall regime, with less than 150 mm per annum, supplemented by fog and dew. Strong, cool southwesterly winds alternating with hot, dry northeasterly winds also influence life in this desert. Lying mostly below 500 masl, isolated inselbergs and mountains rise to 2,000 masl. The characteristic plant growth forms of this ecoregion include stem-, leaf- and root-succulents belonging to the families Apocynaceae, Crassulaceae, Geraniaceae, Portulacaceae and Zygophyllaceae (Figure 23). Grasslands cover extensive plains and intermontane basins towards the interior, with species of Stipagrostis dominating.

Ecoregion 98. Kaokoveld Desert (Barbosa 28, 29; Giess 1; Huntley 15; Atlas of Namibia Team 1–3; Landscape Units 6, 11).

The Namib Desert extends from the Carunjamba River in Angola to the Orange River. On the basis of its rich floral endemism, a northern (Kaokoveld Desert) ecoregion has been distinguished from the species-poor southern (Namib Desert) ecoregion. These ecoregions form a narrow (20–100 km) wedge between the Atlantic Ocean and the coastal plains, hills and inselbergs that skirt the escarpment

(Figures 24–26). They fall peripherally within the HEAN area, as minor outliers on inselbergs and the slopes of escarpments. Characterised as a hyperarid desert, these two ecoregions receive less than 150 mm rainfall per annum, with much of the area receiving half of this amount. Mobile dunes and hard calcrete, gypsum and gravel plains lie between the



Figure 24: Ecoregion 98. Kaokoveld Desert. Large-leaved deciduous trees such as Cyphostemma currorii succeed in the most arid parts of the Namib by exploiting infrequent rain through rapid photosynthesis via their large leaves and water storage in their fleshy trunks. Photo: Ernst van Jaarsveld.



Figure 25: Ecoregion 98. Kaokoveld Desert. Intermontane plains on the margins of the Serra Tchamalindi, Iona National Park. Photo: Merle Huntley.



Figure 26: Ecoregion 98. Kaokoveld Desert. Mixed Commiphora and Acacia savanna at the interface between the Namibian Savanna Woodlands and Namib Desert ecoregions, Iona National Park, Namibe. Photo: Ernst van Jaarsveld.

sea and intermittent sandy plains and rocky hills of the interior. The dunes have little if any vegetation. Inland, succulent shrubs, thorny bushes and low trees of Acacia, Commiphora, Euphorbia, Rhigozum, Sesamothamnus and Sterculia are scattered across a matrix of sparse, short grasses of Stipagrostis species. The iconic gymnosperm Welwitschia mirabilis is locally common in the Kaokoveld Desert. Despite its aridity, the desert is home to a rich diversity of vertebrate and invertebrate species, many of these demonstrating complex adaptations to life in an almost waterless environment.

Ecoregion 103. Namib Desert (Giess 2, 3; Atlas of Namibia Team 3; Landscape Unit 11).

The vegetation includes a mix of Karoo-Namib and Zambezian floristic elements. Vegetation-less dunes occur along the coast, with gravel plains occupied by dwarf shrublands to the interior, succeeded by ephemeral grasslands on the sandy plains of intermontane basins. The rocky hills to the east have mixed open woodlands and a light cover of grasslands (Figure 27). Following rare rainfall events, annual forbs proliferate, including species of *Aizoanthemum*, *Helichrysum*, *Mesembryanthemum*, *Senecio* and *Zygophyllum* and species of both annual and perennial grasses. The plains of the southern Namib have a thin mantle of sands, gravel and calcrete, interrupted occasionally by rocky outcrops and hills, with inselbergs rising to over 1,000 masl.



Figure 27: Ecoregion 103. Namib Desert. Stipagrostis grasses dominate the plains of the Pro-Namib as they meet the western scarp of the Naukluft Mountains. Acacia riverine woodland demarcates a linear oasis through the desert. Photo: John Mendelsohn.

ACKNOWLEDGEMENTS

My thanks to John Mendelsohn for his valuable contributions to this chapter and to leading the conceptualisation and production of the monograph, and to him and to Peter Cunningham, Merle Huntley, António Martins, John Pallett, Pedro Vaz Pinto and Ernst van Jaarsveld for the use of photographs.

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