BIODIVERSITY OF THE ZAMBEZI BASIN

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1. INTRODUCTION

The Zambezi River Basin lies across southern tropical Africa, with significant portions in Angola, Zambia, Zimbabwe, Malawi and Mozambique and smaller portions in Namibia, Botswana and Tanzania (see Figure 1). Its total extent is approximately 1.33 million km^2 (Hughes & Hughes 1992). The Zambezi River itself rises in northwestern Zambia on the Central African Plateau which covers much of the continent. It first drains south then eastwards, and exits into the Indian Ocean north of Beira in Mozambique.

The catchment of the main river and a myriad of tributaries – such as the Kafue, Kwando, Gwayi, Manyame, Mazoe, Luangwa and Shire – is underlain by ancient rocks of Triassic and Jurassic age (more than 120 million years old). Although the majority of the basin is covered by woodland and savanna vegetation, interspersed with grasslands and wetlands where drainage is poor, from a biodiversity perspective there are small but significant areas of other habitats such as montane grasslands and shrublands, forests and deep water lakes.

In this paper an outline of the evolution of the Zambezi Basin is given, followed by an account of our knowledge on the vegetation types, plants, vertebrates and invertebrate species found there. Particular reference is given to those species of ecological or economic significance. Areas and species of particular interest from a conservation viewpoint are mentioned, and the conservation threats are outlined.

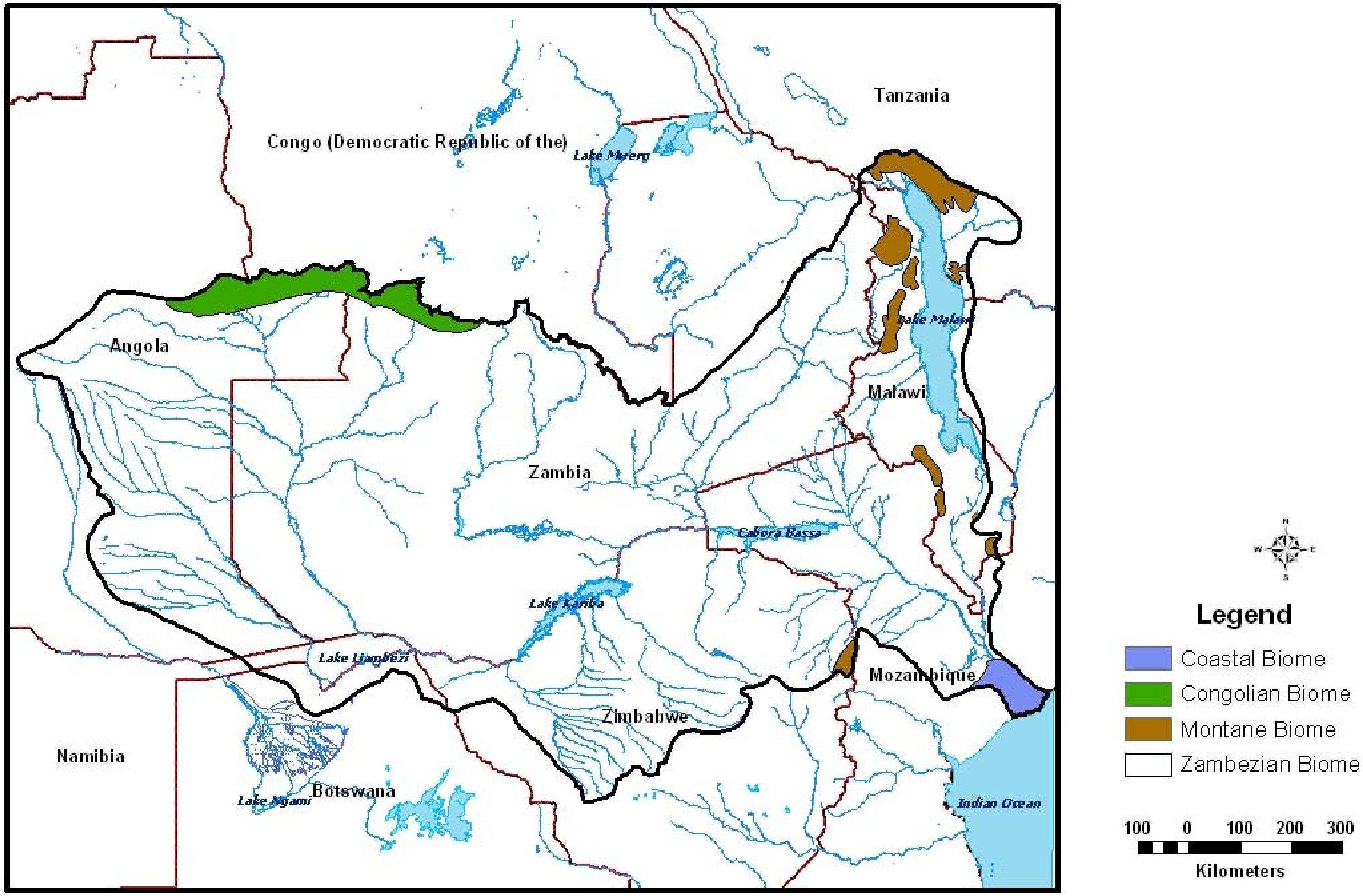
2. THE ZAMBEZI BASIN

2.1 *Zambezian Biomes*

In broad biodiversity terms there are four main biomes across the basin – a Congolian biome, a Zambezian biome, a Montane biome and a Coastal biome (Figure 1, Table 1).

(a) The Congolian biome is that area associated with the headwaters of the Zambezi in northwestern Zambia and northeastern Angola with a moister and warmer climate than that of the rest of the plateau portion of the basin. Here the vegetation and species are a mix of those found in the forested Congo Basin and those found in the less tropical, more wooded, Zambezi Basin.

Fig.1. Biomes of the Zambezi Basin



(b) The Zambezian biome covers the great majority of the basin, around 95%, and comprises woodland, grassland, swamp and lakes. The climate is strongly seasonal with a marked dry season. Frost often occurs on flat ground on the plateau. This biome is sometimes subdivided into moister areas with miombo broad-leaved woodland, and drier areas with mopane or *Acacia* woodland.

(c) The Montane biome lies above 1800-2000 m altitude and is cooler, wetter, often shrouded in mist, and with a much more temperate climate. The vegetation and species are generally similar to those found along the Eastern escarpment mountains, the series of mountains which stretch from Ethiopia through Kenya, Uganda and Tanzania down to the Drakensberg in South Africa and the southwestern Cape.

(d) The Coastal biome is essentially that small part of the basin where climate is modified by proximity to the coast – the delta area and immediate hinterland. The dry season is not so marked, temperatures do not fluctuate greatly, and habitats include dry forest and grasslands. Most species found here are widespread along the East African coast from Somalia to northern KwaZulu-Natal.

Table 1. Biomes of the Zambezi Basin.

Zone	**percent of basin**	**Characteristics**
Congolian	1.5	tropical; high rainfall; dry season not marked; mostly forest; links to Congo Basin
Zambezian	95	sub-tropical; marked dry season; mostly moist or dry woodland & grassland
Montane	2.5	temperate; some dry season precipitation; mostly moist forest, heath and grassland; part of Eastern Arc mountains
Coastal	1	tropical; mild stable climate; mostly dry forest, woodland and grassland; part of East African coast

2.2 *Evolution of the Basin*

Many of the patterns seen today in the distribution of species within the Zambezi Basin are the result of historical processes that have occurred over the last few million years (see Timberlake 1998). So an understanding of present-day biodiversity needs to be based on knowledge of changes in the climate, hydrology and geomorphology which have occurred within the region over this period, as well as the modifications to the environment caused by human activity over the last thousand years or so.

Changes in continental climate during the Pleistocene period (2 million years ago to present), caused in part by the Ice Ages in the Northern Hemisphere, have resulted in long periods of aridity across the basin interspersed with cooler periods with higher rainfall. Forest and forest species, which require cooler and moister conditions than are generally found in the basin today, would have been more widespread and not isolated patches or populations as at present, while the extent of savanna woodland would probably have been significantly less. And some areas would have changed less than others due to ameliorating factors such as altitude or proximity to the ocean. Thus the patterns of habitats and species we see today reflect, in part, the greater extent of forest during cooler, wetter periods, the more tropical and stable climate associated with the coastal plain, and the results of the successive waves of dry woodland that washed over the plateau. In addition to these historical factors there is, of course, a great variety of soils, moisture conditions, temperatures and landscape, all of which are reflected in different habitats, vegetation types and species composition.

Owing to a series of river captures over the last few million years, the Zambezi landscape has been much modified, and this hydrological evolution of the river system is often reflected in species distribution (Timberlake 1998), particularly that of aquatic species or those dependent on water bodies. The present-day Zambezi system can be divided up into three separate sections, each differing in its landscape characteristics, its geological history and its biodiversity. These are the Upper Zambezi, the Middle Zambezi, and the Lower Zambezi. The Lake Malawi catchment is often considered part of the Middle Zambezi, although it does have its own unique characteristics.

The Upper Zambezi is geomorphologically the oldest part of the basin and has probably not changed substantially for some 2-5 million years. The early Zambezi River, the proto-Zambezi, drained a vast area of the Central African Plateau, including the Bangweulu Swamps and Lake Mweru in northern Zambia. The Kafue, Kavango and other rivers drained towards the present-day Caprivi, where a series of huge inland lakes were thought to exist (Shaw & Thomas 1988, Thomas & Shaw 1988, 1991). Waters overflowing from here flowed into what are now the Shashe and Limpopo rivers, and exited to the sea north of present-day Maputo. Between 1.5 and 0.5 million years ago, a series of river captures took place in northeastern Botswana owing to slight earth movements, which eventually resulted in all the waters from the Upper Zambezi flowing eastwards into the Gwembe Trough – occupied today by Lake Kariba. Perhaps somewhat earlier than this the Chambeshi River (which now goes on to form the Bangweulu Swamps) and other headwaters were "captured" by aggressive southern tributaries of the Congo.

This vast inland drainage basin was, and is, geomorphologically mature with little relief. Species have few biological barriers to cross, and wetland organisms in particular could move along slow waterways and broad floodplains over a large part of the sub-continent.

The Middle Zambezi, that part of the basin between Victoria Falls and the Lupata Gorge downstream of Tete in Mozambique, is much younger, more environmentally heterogeneous, and much smaller in extent than the Upper Zambezi. It includes the Luangwa Valley and most of northern Zimbabwe, although not the Kafue Flats. Lake Malawi, its catchment and the Upper and Middle Shire, are often considered to be part of the Middle Zambezi, although they are a biologically separate unit as regards aquatic biodiversity. Prior to the capture of the Upper Zambezi, this section would have been relatively small, typified by narrow floodplains, rapids and large fluctuations in seasonal flow, with a wide range of vegetation types from evergreen forests on the flanks of the high peaks through mesic woodlands on the watershed and higher ground, to drought-adapted deciduous woodlands (mopane and acacia) in the lower-lying broad valleys. Today, it is a dissected landscape, ranging from mountains and other high land down to broad dry valleys typically covered in mopane and other forms of drought-adapted deciduous woodland. Its biological character has been greatly modified in recent years by the construction of two huge dams – Kariba and Cabora Bassa – and a series of smaller dams on the tributaries, particularly in Zimbabwe.

The Lower Zambezi extends from the Lupata Gorge in Mozambique to the coast where the river exits at Chinde, and also includes those parts of the Shire River in Malawi below the Kapichira Falls near Blantyre. This section of the Zambezi is typified by a broad floodplain, often with many parallel channels and shifting sandbanks, while the coastal portion includes extensive grasslands and freshwater swamps, dunes and mangroves. Although its geological history is not clear, this part of the basin has biological similarities to the Pungwe/Buzi system, and it is linked during floods to the Gorongosa area and Urema Trough.

2.3 *Biodiversity Studies*

The biodiversity of the basin as a whole has not been comprehensively documented. Studies have been concerned principally with individual groups or with individual countries rather than the whole basin. However, a comprehensive review of various animal and plant groups over southern Africa, including the Zambezi Basin, was compiled by Werger (1978), and this remains perhaps the most valuable document to date. The flora and vegetation map of the Flora Zambesiaca area (Botswana, Caprivi, Malawi, Mozambique, Zambia, Zimbabwe) also covers the major part of the basin, but most major regional studies on birds or mammals (e.g. Maclean 1993, Smithers 1983) use the Zambezi River as a northern boundary. Thus it is difficult to compile a clear picture of biodiversity across the basin from existing literature except by a long, labourious process of accumulation – group by group, and area by area. Recently, however, a comprehensive regional synthesis of published information on biodiversity and ecology relating to the wetlands of the basin has been produced (Timberlake 1998), which can form the basis for an enlarged study of the biodiversity of all its ecosystems. This has been followed by a comprehensive review of many wetland taxonomic groups stating our present knowledge on wetland diversity and its distribution (Timberlake 2000).

3. VEGETATION TYPES

The vegetation of the Zambezi Basin is very varied, as would be expected of such a large area spanning mountain top to the coast. The main map on African vegetation is that by Frank White (1983) whilst the map of the Flora Zambesiaca area (Wild & Barbosa 1967), together with the similar vegetation map of Angola (Barbosa 1970), cover all but 3% of the total area.

In terms of broad vegetation types, almost half of the basin is classified by White as wetter or drier miombo woodland, part of the Zambezian biome. Miombo is a type of woodland dominated by trees of the genera *Brachystegia, Julbernardia* or *Isoberlinia* with a well-developed grass layer. Other widespread vegetation types are mopane woodland (dominated by mopane, *Colophospermum mopane*), mosaics of various types of woodland, dry forest (including that dominated by Zambezi teak, *Baikiaea plurijuga*) with grassland, and open woodland dominated by various species of *Acacia*. Amalgamating some of White's units, the vegetation of the basin can be described under eight broad types (Table 2, Figure 2).

Both miombo and mopane woodland are not particularly species-rich, nor do they contain many species of restricted distribution. Hence they are sometimes overlooked by conservationists. But this hides their major economic value to those dependant on natural resources for survival.

The vegetation of the Montane biome is both species-rich and shows a marked difference from surrounding areas. It is restricted, within the basin, to the Misuku Hills, Nyika Plateau, Shire Highlands and Mt Mulanje in Malawi and the Nyanga mountains in Zimbabwe. Mt Gorongosa in Mozambique and the Vumba and Chimanimani mountains in eastern Zimbabwe are just outside the basin. Vegetation types found in these upland areas are rainforest, montane grassland and a fynbos-like shrubland on the highest plateaux. This biome, with its specific range of habitat characteristics and island-like nature, supports some endemic plant and animal species (i.e. species not found elsewhere).

Other vegetation types of restricted distribution and high conservation interest are the dry forests of Barotseland on Kalahari sands (dominated by the tree *Cryptosepalum pseudotaxus*) and the hot, dry parts of the Zambezi and Shire valleys (characterised by *Combretum* shrubs and trees such as *Xylia torreana*, *Pterocarpus antunesii* and *Pteleopsis* species).

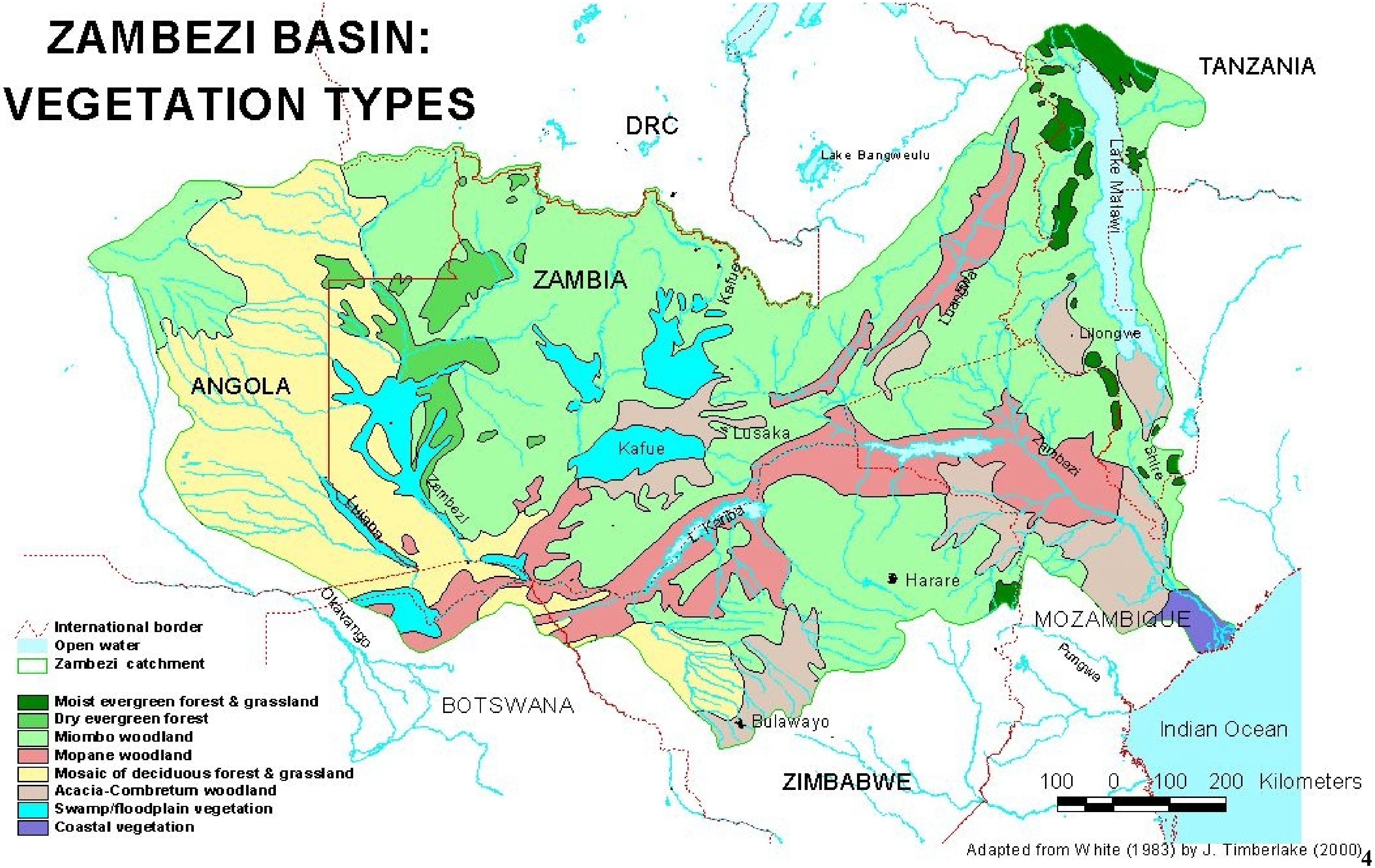
Table 2. Broad vegetation groups of the Zambezi Basin (derived from White 1983).

vegetation group	**biome**	**White's units**	**% of ZB**
miombo woodland	Zambezian - wet	25,26	49
woodland/dry forest/ grassland mosaic	Zambezian - wet	22a,47,60	19
dry evergreen forest	Zambezian - wet	6	3
swamp & pan	Zambezian -wet	64,75,76	4
mopane woodland	Zambezian - dry	28	12
Acacia/mixed woodland	Zambezian - dry	29	7
montane forest/grassland	Montane	19a	2
coastal forest/woodland/ grassland mosaic	Coastal	16a	1
lake		-	3

Swamp and floodplain vegetation types cover only a small part of the basin, but can be of significant economic importance for fishing, materials for crafts and for livestock grazing. They are often the focus of human settlements owing to the availability of water year-round, as well as being a regular source of protein in the form of fish. However, from a biodiversity viewpoint they are not particularly rich and many of the species are widespread in similar environments across the continent. The floodplains of the Upper Zambezi though, an ancient stable environment, have been a focal point of much evolution and species radiation.

4. PLANTS

Knowledge on the distribution of plant species across the basin is not comprehensive, primarily as large areas are still very poorly recorded (especially in the upper reaches and in the coastal plain). Based on a figure of 9000-10,000 species of flowering plants and ferns in Flora Zambesiaca area (G. Pope, pers. comm.), it is estimated there are between 6000 and 7000 species in the Zambezi Basin.


ZAMBEZI BASIN:
VEGETATION TYPES
DRC
TANZANIA
Lake Bangweulu
Lake Malawi
ZAMBIA
Kafue
Luangwa
Lilongwe
ANGOLA
Lusaka
Kafue
Zambezi
Shire
Zambezi
Lungwebungu
L. Kariba
Harare
Okavango
MOZAMBIQUE
Pungwe
International border
Open water
Zambezi catchment
Moist evergreen forest & grassland
Dry evergreen forest
Miombo woodland
Mopane woodland
Mosaic of deciduous forest & grassland
Acacia-Combretum woodland
Swamp/floodplain vegetation
Coastal vegetation
BOTSWANA
Bulawayo
Indian Ocean
ZIMBABWE
100 0 100 200 Kilometers
Adapted from White (1983) by J. Timberlake (2000)

4

Patterns of plant species distribution in Africa have been described by White (1983). He divided up sub-Saharan Africa (excluding the Cape and Madagascar) into 14 phytochoria, or broad areas of associated plant species within which many are endemic. The Zambezi Basin forms part of three of these phytochoria – the Zambezian regional centre of endemism, the Zanzibar-Inhambane regional transition zone, and the Afromontane centre of endemism – which correspond with the Zambezian, Coastal and Montane biomes describe earlier. White also recognises the presence of elements from the Congolian biome in the headwaters area, but calls it the Guinea-Congolia/Zambezi regional transition zone.

4.1 *Wetland Plants*

Plant species found in swamps and permanently wet places tend to be highly adapted, and readily dispersed by water and birds, hence are often widespread. Species found in seasonally flooded areas, such as dambos and floodplains, are less highly adapted and are also less likely to be distributed widely by birds or water currents. The ancient floodplains of the Upper Zambezi have been the site of speciation in groups such as bulbous plants and the so-called "underground trees" or suffrutices (White 1976). The latter are species of woody plant which have evolved from various tree species, independently of each other, to overcome the rooting impediments of a poorly drained subsoil and frequent fires and frosts. Instead of growing a large woody, above-ground trunk, the trunk has been effectively forced underground and ramifies extensively just beneath the soil surface. The great majority of the 98 recognised species in southern Africa, including *Parinari capensis*, *Annona stenophylla*, *Cryptosepalum exfoliatum*, *Trichilia quadrivalvis* and *Syzygium guineense* subsp. *huillense*, are found on the floodplains of the old Upper Zambezi or in associated areas of Kalahari sands.

Wetland plants of particular economic importance include papyrus (*Cyperus papyrus*), rushes (*Typha*) and reeds (*Phragmites*), all of which are used in construction or craft-making. They are of particular importance in wetland areas owing to the general paucity of trees and wood. Species of water lily (*Nymphaea*) are also used as a source of food in times of shortage. There are some introduced wetland plants of negative economic importance as they can block water channels, cause fish mortality and provide suitable breeding grounds for bilharzia-carrying snails and mosquitoes. These include the Water Hyacinth (*Eichhornia crassipes*), Water Lettuce (*Pistia stratiotes*), Kariba Weed (*Salvinia molesta*) and the Water Fern (*Azolla*).

4.2 *Woodland Plants*

Woodland covers most of the Zambezi Basin and it is in woodland (or previously wooded) areas that the majority of the basin's population live. The major woodland tree species are *Brachystegia*, *Julbernardia*, Mopane and Zambezi Teak. Locally other genera such as *Acacia*, *Combretum* and *Terminalia* are important.

Species composition depends primarily on climate and soil type. On the deep Kalahari sands in the west of the basin, Zambezi Teak is common, often mixed with *Brachystegia spiciformis*, while in the lower, drier areas of the valley floors on clay-rich soils, mopane is dominant. Miombo woodland comprises most of the remaining woodland area with *Brachystegia spiciformis* being particularly widespread, and *Julbernardia globiflora* in drier areas (south of the Zambezi or on stony soils). *Julbernardia paniculata* and other species of *Brachystegia* are common in the north under wetter, warmer conditions.

Important products of these woodland types are wood (both for construction and for firewood), honey, grazing and in the provision of a habitat for wildlife. Many of the soils are suitable for agriculture, and the ability of cut trees to coppice reduces soil erosion and restores fertility through bush fallow. Mopane is greatly desired as a strong termite-resistant construction wood and for firewood, while species such as Zambezi Teak, False Mopane or Mchibi (*Guibourtia coleosperma*) and Bloodwood, Mukwa or Kiaat (*Pterocarpus angolensis*) have been heavily exploited for commercial timber (furniture, parquet blocks, railway sleepers, etc.). Other important timber species include Muwanga (*Pericopsis angolensis*), Pod Mahogany (*Afzelia quanzensis*), African Ebony (*Dalbergia melanoxylon*), Panga Panga (*Millettia stuhlmannii*) and Leadwood (*Combretum imberbe*).

4.3 *Montane and Forest Plants*

The area of the basin covered by montane vegetation, rainforest and dry forest or thicket is comparatively small, but these areas contain almost half of the plant biodiversity, and most of the species of restricted distribution.

Montane vegetation starts at about 1800-2000 m altitude and such areas have been likened to islands in a sea of savanna woodland. Perhaps because of this there has been a certain amount of speciation and there are a number of plant species restricted to, or endemic to, certain mountains – particularly the Nyika Plateau and Mt Mulanje. Many of these species are grassland herbs from widespread genera, and are not normally woody plants. The fynbos-like shrublands on the highest plateaux in the Nyanga area have a lot of similarities to the fynbos of the Cape, although they have nowhere near that level of species diversity. Species found in the Montane biome are generally restricted to these habitats, although some occur throughout the string of Eastern Arc mountains. Owing in part to the inhospitable environment there are no species of economic interest and few threats, other than from invading trees such as wattle (some *Acacia* species) and pine (*Pinus* species), but the conservation interest and importance is very high.

Rainforest is only found in the Zambezi Basin where local rainfall or climatic conditions allow it to develop – the climate is generally too dry. Such conditions are found in sheltered gullies or on the gentle windward slopes of mountains. Forests are very rich in plant diversity, both herbaceous species and trees, and because so much of the original forest extent has been cleared for agriculture they are of major conservation interest. The economic significance of forests is in providing valuable timbers such as Red Mahogany (*Khaya anthotheca*), in protection of catchments from erosion and in provision of materials for traditional medicine and craft-making.

Another category of forest is that fringing rivers and drainage lines throughout the woodland areas. Most of the broad seasonal rivers have a fringe of large trees such as Winter Thorn (*Faidherbia albida*), Natal Mahogany (*Trichilia emetica*), *Acacia* and Waterberry (*Syzygium*), but in many places these fringes are being destroyed by clearance for agriculture or for wood. Riparian fringes are an important wildlife habitat and corridor and also protect river banks from erosion. Most of the plant species found there are widespread in similar habitats elsewhere although some are curiously restricted in distribution. The conservation and economic value of riparian forest is relatively high.

At the headwaters of the Zambezi in Mwinilunga District in Zambia and in northeastern Angola, the gallery or riverine forests have a different species composition to those further downstream with species more typical of the Congo Basin such as *Marquesia*, *Berlinia giorgii* and *Lannea antiscorbutica*. These species are of great conservation interest from a basinwide perspective as they are so limited in occurrence here. The different species composition of this area is also mirrored in the biodiversity of other groups such as birds, small mammals, dragonflies and butterflies.

At the mouth of the Zambezi and along tidal creeks are mangrove swamps consisting of specialised trees such as Red and White Mangroves (*Rhizophora mucronata* and *Avicennia marina*) and *Lumnitzera racemosa*. These species are widespread along the

East African coast, but are of significant biodiversity interest from a basinwide perspective. Mangrove areas are not species-rich owing to the high level of adaptation required to survive in a saline environment, but are significant economically as the trees provide good quality construction wood, help reduce shoreline erosion and provide a suitable habitat for fish breeding.

5. VERTEBRATES

Zoogeographically, the Zambezi Basin is considered to be in the Afrotropical (formerly Ethiopian) realm and shows similarities in its fauna to many parts of the savanna or woodland zone of southern and eastern Africa. There are no major centres of endemism or particular "hot spots" for most groups, apart from Lake Malawi for aquatic organisms, although the montane and moist forest habitats support some species not found elsewhere in the basin. To the four biomes described earlier, Lake Malawi can be added as a fifth, but only as regards solely aquatic organisms such as fish and molluscs associated with this deep water lake. Estimated numbers of species of the various groups, and areas of particular richness, are indicated in Table 3.

5.1 *Mammals*

The Zambezi Basin is renowned for its assemblage of large mammal species such as elephant, buffalo, giraffe, lion and, until recently, rhino. Compared to East Africa there is a preponderance here of browsers rather than grazers as the basin is mostly woodland rather than highly productive grasslands associated with the East African Rift Valley. The total number of mammals recorded from the basin is around 195 (A. Brock-Doyle, pers. comm., plus additions).

Some of these species, such as the colobus monkey, samango monkey, blue duiker and various rodents, are restricted to moist forests in the eastern part of the basin, while the tree pangolin is only found in the gallery forests of the Zambezi headwaters. A group of particular interest, almost endemic to the palaeo-basin, is the lechwe antelope. Although often considered as subspecies, it is likely the three living groups should be considered full species (F. Cotterill, pers. comm.). The black lechwe is endemic to the Lake Bangweulu area in northern Zambia, as was the (now extinct) Roberts' lechwe, which was part of the palaeo-Upper Zambezi, and the Kafue lechwe is restricted to the Kafue Flats in southern Zambia. The red lechwe is more widespread, but is principally confined to the Zambezi Basin. Another species of Reduncine antelope confined to floodplains and wetlands is the puku, which has the Zambezi Basin as its centre of distribution. It would appear that an early form of the lechwe which inhabited the wetlands of the old basin split up some hundreds of thousands of years ago into different populations, which later became isolated and started to speciate.

Table 3. Number of species within the Zambezi Basin for various biological groups and areas of high diversity.

group	no. species	areas of high diversity
flowering plants	6-7000	headwaters, Barotseland, Mt Mulanje, Gorongosa
lower plants	?? (200 ferns)	Mt Mulanje, Nyanga
mammals	c.200	headwaters, Mid Zambezi, Luangwa
birds	c.700	Kafue
reptiles	200	headwaters, Barotseland, L.Malawi
amphibians	90	headwaters, Barotseland, L.Malawi
fish	165 (+L.Malawi)	L.Malawi
dragonflies	210	headwaters, Okavango
butterflies	1100	headwaters, Eastern mountains
freshwater molluscs	100	L.Malawi

5.2 *Birds*

The birds of the basin are comparatively well-known. There are probably around 700 species of bird recorded (P.J. Mundy, pers. comm.), of which probably only 15-20 are endemic to the basin, including the Black-cheeked Lovebird (*Agapornis nigrigenis*) and the Slaty Egret (*Egretta vinaceigula*). Of these species about 167 are considered to be wetland-related, while birds confined to montane forests include Swynnerton's Robin (*Swynnertonia swynnertoni*), Chirinda Apalis (*Apalis chirindensis*) and Roberts' Prinia (*Prinia robertsi*). Within the Zambezian biome, the division between wetter miombo woodland and the drier mopane and *Acacia* woodlands is clearly reflected in bird species composition.

The wetlands and other habitats of the Zambezi Basin are important sites for Afrotropical migrants (c.70 species) and Palaearctic migrants (c.90 species) – those species that come to southern Africa to breed, or breed in the northern summer in Europe, Russia and Asia, but spend the northern winter in Africa as non-breeding migrants, respectively. Examples of Afrotropical migrants of particular interest and concern are the Rock Pratincole (*Glareola nuchalis*), African Skimmer (*Rynchops flavirostris*) and Carmine Bee-eater (*Merops nubicoides*) along the Zambezi

River, and the Blue Swallow (*Hirundo atrocaerulea*) on montane grasslands. Palaearctic migrants of interest and concern include the White Stork (*Ciconia ciconia*), harriers (*Circus* spp.), Lesser Kestrel (*Falco naumanni*), Corncrake (*Crex crex*) and Black-winged Pratincole (*Glareola nordmanni*). Perhaps the bird species that best epitomises the conservation concerns is the Wattled Crane(*Bugeranus carunculatus*) – about 95% of the world population of 13-15,000 birds are dependent on the floodplains and dambos of the Zambezi Basin and nearby areas.

Birds of economic significance include the ducks and geese, many of which are hunted for meat. Some wetland areas of the basin, such as the Kafue Flats, have great concentrations. Francolins and guineafowl are also hunted for food in many areas. Species of negative importance include the Red-billed Quelea (*Quelea quelea*), which can devastate small grain crops in some areas in a short period of time.

5.3 *Fish*

The fish species of the basin have been fairly well documented, principally owing to their economic interest, although details of the fish diversity of the Zambezi Delta are still scanty. There are about 165 species of freshwater fish recorded from the basin plus perhaps 500 endemic species (mostly cichlids) in Lake Malawi. Of this total, 42% are found only in the old Upper Zambezi system (including the Kafue), 36% are found only in the Middle and Lower Zambezi, while the remainder are common to both (B. Marshall, pers. comm., Skelton 1994). The lungfish, eels and Zambezi shark are all found only in the Lower and Middle Zambezi.

With the exception of the Lake Malawi cichlids, which are often endemic to just one stretch of shoreline or island, most fish species are relatively widespread. Only 15 species have a limited distribution (B. Marshall, pers. comm.). From a conservation point of view, Lake Malawi is not just of basinwide importance but significant worldwide. How such explosive speciation came about, much of it perhaps only in the last few hundred years (Owen *et al*. 1990) is not clear, but the large rise and fall in lake level over recent millennia, isolating populations previously freely interbreeding, the important role of body colouration and sexual selection, and the high reproductive rate are probably key features.

Economically, fish are of major importance in areas around dams and along major rivers. The Lake Tanganyika sardine, or kapenta, was introduced into the filling Lake Kariba in the early 1960s, and more recently into Cabora Bassa, and now forms the basis for an enormous commercial fishing industry. The species was so successful because there was a niche created for it, but concerns have been expressed over its proposed introduction into the pelagic (=open water) environment of Lake Malawi. Here it may well compete for the aquatic invertebrates that form the main diet of many of the endemic cichlids.

5.4 *Reptiles and Amphibians*

Knowledge on the biodiversity of reptiles and amphibians of the basin is comparatively good, although there are still large gaps in our knowledge of distributions. There are 200 species of reptile and around 90 species of amphibian recorded. Only very few are endemic to the basin or areas within it. As with the fish, the Upper and Middle/Lower Zambezi have clear differences in species composition, with 44% of the 160 wetland-related species confined to the Upper Zambezi, 22% confined to the Middle/Lower Zambezi, and the remainder common to both. Barotseland has a particularly rich herpetofauna as it is where three broad zoogeographical zones meet – the wetter, more tropical Angolan/Congolian zone, the drier Kalahari zone and the East African coastal zone. There are a number of species, particularly reptiles, that are confined to the coastal plain but just come up onto the extensive Central African Plateau.

6. INVERTEBRATES

Invertebrate biodiversity is not well known in the Zambezi Basin except for a few groups including dragonflies (Odonata), butterflies (Lepidoptera), freshwater molluscs, dung beetles and grasshoppers/crickets (Orthoptera). Instead, groups of particular economic interest – mosquitoes, tsetse fly, locusts, ticks and agricultural pests – have been the focus of detailed research. The number of species of insects and other invertebrates present in the basin is unknown, but it is likely to be tens if not hundreds of thousands.

Dragonflies are a group of insects that are principally confined to water and wet places where they breed. Of the 210 species recorded from the basin, 136 are widespread in the Afrotropics while 74 appear to have limited distributions (M. Fitzpatrick, pers. comm.). Collecting has been localised with many large gaps remaining, particularly Barotseland, but the richest area in terms of species number and endemics appears to be the Zambezi headwaters. Eleven species of Congolian affinity, apparently endemic, are found there. The Okavango Delta in Botswana, just outside the basin, has been well collected and contains seven species that have not been seen elsewhere. Dragonflies have little economic significance as such, but are known to be useful indicators of wetland health.

Butterflies are another comparatively well studied group. There are around 1100 species recorded from the Zambezi Basin (A. Gardiner, pers. comm.). The richest area is again the headwaters around Mwinilunga where 340 species have been recorded. The forest and montane areas, and those where the Congolian elements come into the basin, are the most different and most diverse from the predominantly woodland remainder. The group has little economic value although butterflies can indicate environmental health – the loss of certain species indicates generally that their food plant has been lost from that habitat.

Tsetse flies are a major economic concern as some species carry human sleeping sickness, and most transmit the near-fatal trypanosomiasis to cattle and other livestock. Thus in an area where tsetse is present, even at low levels, it is not possible to keep cattle (hence the use of draft power is excluded) except under a drug regime. Knowledge of tsetse fly ecology and distribution is fairly good for much of the basin, but less so in Mozambique and Angola.

Freshwater molluscs have been comparatively well-studied across the basin as some species are intermediate hosts of the parasite which causes schistosomiasis or bilharzia. Of the 98 indigenous species recorded from the basin, 47 are found in Lake Malawi (C. Dudley, pers. comm.). Of these 98 species, 28 are endemic to the basin including 23 endemic to Lake Malawi, showing the biodiversity importance of this unique lake. The Afrotropics as a whole contain 382 species of mollusc. The patterns of species distribution show similarities to those for fish with a very distinct fauna for Lake Malawi, a distinct East African coastal element, and an Upper and Middle/Lower Zambezi element. The Congo Basin supports a much higher number of freshwater molluscs than the Zambezi, probably because of its greater stability over the last few million years. There are also a significant number of species in common.

7. AREAS OF INTEREST

Areas of particular interest for biodiversity can be selected from a basinwide perspective or from a continental perspective. From a continental or worldwide viewpoint there are perhaps four areas of particular conservation significance: (a) Lake Malawi, (b) the swamps, floodplains and woodlands of the palaeo-Upper Zambezi, (c) the Middle Zambezi and Luangwa valleys, and (d) the Gorongosa/Cheringoma/Zambezi Delta area. These are described in more detail below.

(a) Lake Malawi is the southernmost of the deep-water lakes associated with the formation of the East African Rift Valley, the others including Lake Tanganyika. These lakes are of moderate antiquity and, despite major fluctuations in water level over the centuries (see Owen *et al*. 1990) have been the sites of much evolutionary radiation, especially in some fish groups and freshwater molluscs. Lake Malawi is the only place in the basin with a natural pelagic (open water) habitat, as Lakes Kariba and Cabora Bassa are very recent and man-made. There are thought to be around 500 species of fish, nearly all cichlids, in the lake, with about 98% endemism (i.e. the species are not found elsewhere). The number of freshwater mollusc species is around 47 with 50% endemism. This high species number and level of endemics is not reflected in other groups, however.

(b) The old, stable plateau of the palaeo-Upper Zambezi, covering the floodplains and swamps of Barotseland, Busangu, Kafue, Okavango and Bangweulu, as well as the associated woodlands on higher ground, have also been the sites of evolutionary radiation in a range of groups. It appears as if some of the Reduncine antelope speciated here, many of the underground trees or suffrutices, and bulbous plants in a range of genera, and possibly other groups. The Barotse floodplains are particularly rich in reptiles and amphibians as it is here that three centres of distribution meet – the Kalaharian, the Congolian and the East African coastal. These floodplains, dambos and grasslands are some of the most extensive and least disturbed left on the continent. The miombo, teak and *Cryptosepalum* woodlands on Kalahari sands in the west of the area are also of significant biodiversity interest.

(c) That section of the Middle Zambezi Valley from Kariba downstream to Cabora Bassa, and the Luangwa Valley in Zambia are two of the last remaining extensive protected areas for large mammals. They contain vegetation typical of hot dry valleys, such as mopane woodland, *Combretum* thickets and riparian fringing woodland. Its interest is not in their biodiversity as such, or in unusual species, but in its potential to support reasonable populations of large mammals such as elephant, rhino and buffalo which are under threat elsewhere.

(d) The Mt Gorongosa–Urema Trough–Cheringoma Plateau–Zambezi Delta area is extensive but covers an enormous diversity of habitats from mountain to mangrove (Tinley 1977), not found in such proximity elsewhere on the continent. Mt Gorongosa, although just outside the Zambezi Basin, supports a wide range of montane and forest species, and the valley floor of the Gorongosa National Park has, in the recent past, supported large numbers of wildlife. The Cheringoma Plateau, clothed in miombo woodland and dry forest containing many unusual species, rises up on the other side and then gently descends to the extensive grasslands of Marromeu, coastal dunes and mangrove swamps. Over this large area not only can viable populations of a multitude of species survive, but the ecological processes that sustain such a landscape can continue to operate.

At a more detailed level there are a number of smaller sites of biodiversity interest. The headwaters around Mwinilunga are very rich biologically, containing many species not found elsewhere in the basin. The Kafue Flats are a well studied wetland system that not only supports an endemic lechwe antelope but also hosts seasonally vast numbers of waterbirds, including Palaearctic migrants. Mt Mulanje in southern Malawi supports extensive and rich rainforests on its slopes and a number of endemic plants up on the plateau. Although the Okavango Swamps, the largest and richest swamps in the region, are outside the present-day basin, they have been joined hydrologically and are still joined biologically.

8. THREATS TO BIODIVERSITY

Threats to biodiversity conservation take many forms, some direct and obvious, others indirect and subtle, and can be grouped into six categories: (a) overexploitation, (b) land clearance, (c) dams and modification of hydrology, (d) introduction of exotic species, (e) fire, and (f) pollution.

(a) Overexploitation occurs when humans use a particular species or group of species beyond the point where that species can replace itself. It is usually localised when viewed on a basin level, but has been severe and more widespread in some cases. Examples include the destruction of large mammals such as elephant, rhino and antelope over extensive areas, particularly during the latter part of the last century and the first few decades of the current one; extraction of valued timber such as mukwa, African Ebony and Zambezi Teak; fish from Lakes Malombe and Malawi and the Lower Shire; and grass from some grazing lands in Zimbabwe. Generally, if small populations of the exploited species remain, the effects of overexploitation are reversible given time and protection.

(b) When settled human populations expand and require more land for urban development or for arable agriculture, or when new technologies (e.g. draft power, tractors) are introduced allowing people to farm larger areas, land clearance becomes a major concern. If fields are stumped and ploughed (as opposed to the slash-and-burn *chitemene* system still practised in miombo woodland in Zambia) and the area is on readily-erodible soils, the process is irreversible over human time scales of 20-50 years. That is, even when fields revert to bush fallow the vegetation does not revert to the former structure and species composition, but to a new state. In many parts of the basin the vegetation is in a stable state, but probably not what it originally was – as can be seen in the acacia woodlands of Matabeleland in Zimbabwe, in some of the woodlands of the Zambezi Valley, in the sugar plantations of the Zambezi Delta, and possibly in some of the grasslands of Barotseland. Land is still being cleared for agriculture, particularly in what were marginal agricultural areas in the Middle Zambezi Valley, and also for increasing urban populations in Zambia and Zimbabwe.

(c) The construction of dams has had probably the greatest effect on biodiversity of wetland and aquatic species and on wetland ecological processes. These include large dams, such as Kariba, Cabora Bassa, Itezhi-Tezhi and Kafue Gorge, and the myriad of small dams on almost all tributaries of the Zambezi in Zimbabwe. Hydrology is changed, flooding regimes greatly modified, and hence habitat and species composition. Two new major habitats have been created – a pelagic (open water) environment and a littoral (shoreline) environment. Creation of these new environments has led to previously rare species (e.g. freshwater molluscs) becoming abundant (Kenmuir 1980), and to the invasion or introduction of species new to the basin. As slow-water environments are now available in the Middle Zambezi, whereas before they were not, fish species from the Upper Zambezi are now appearing resulting in mixing of two previously separate faunas (Balon 1971, 1974). This will also obviously have evolutionary consequences. Fears have been expressed concerning the effects of flood regulation on wetlands. For example, there were many studies in the 1960s and 1970s (e.g. Williams & Howard 1977) on the Kafue Flats to determine what changes there would be to the Kafue lechwe, waterbirds, fisheries and vegetation. Despite marked changes in relative abundance, it appears that the worst fears expressed have not materialised. The gradual drying up of some of the wetlands of the Zambezi Delta, including the world-famous floodplain grasslands of Marromeu which supported large herds of buffalo, has been ascribed to regulation of the annual flood by Cabora Bassa and Kariba. But the incredible reduction in buffalo numbers since 1970 is primarily due to illegal hunting during the civil war.

(d) The introduction of exotic organisms is a major concern of conservationists. Some exotic species are able to out-compete native species or modify the ecology of a area. Examples include the invasion of pines and wattle trees into the montane grasslands of Nyanga and Mt Mulanje, the introduction of the Nile Tilapia fish (*Oreochromis niloticus*) into the waters of the Middle Zambezi, and Kariba Weed (*Salvinia molesta*) into the Chobe system and Lake Kariba. The introduction of the Lake Tanganyika sardine (*Limnothrissa miodon*) into Lake Kariba in the 1960s has not resulted in loss of biodiversity as a new habitat was created and there were no native species to occupy it. However, fears have been expressed over the possible introduction of kapenta into Lake Malawi where it would feed on lake flies which are the main food for some endemic cichlids, thus possibly endangering these species (Eccles 1985).

(e) Fire has modified vegetation structure and species composition in the moister woodlands with a good grass layer, and in particular in the extensive grasslands associated with floodplains. Large areas of Barotseland are burnt regularly, as are the grasslands of the Zambezi Delta. Soil erosion has increased, and species of plant and animal which cannot avoid fire (by flying away, going underground, or regenerating rapidly) are reduced in distribution and abundance.

(f) Pollution often has an insidious chronic effect on biodiversity rather than a sudden acute effect. However, industry and extensive agriculture are not as prevalent in the Zambezi Basin as they are in South Africa or Europe, and so the extreme effects often noted elsewhere by environmentalists have not really occurred here. Increasing use of fertilizers in agriculture, and large urban populations resulting in large volumes of sewage, have given rise to acute problems of water pollution, such as in Lake Chivero outside Harare. There have been some effects noted on birds owing to the use of DDT for spraying against tsetse fly in the Zimbabwe part of the Zambezi Valley (Douthwaite & Tingle 1994), but many of these effects appear to be reversible and the use of DDT has now mostly stopped. Of perhaps bigger concern for conservation in this case is the increased land clearance and overutilization of natural resources that results from the introduction of cattle into such areas.

Historically, within the Zambezi Basin, the major changes in biodiversity have resulted from land clearance and from overexploitation of certain species of economic value, and for aquatic and wetland species the construction of large and medium-sized dams along the Zambezi River and its tributaries.

SUMMARY

The Zambezi Basin, 1.33 million km^2 in extent, incorporates four distinct biomes and numerous habitats. Although the Zambezian biome covers 95 per cent of the area, the Montane and (especially) the Congolian biomes are exceptionally species-rich.

Many of the patterns of species distribution seen today are the result of historic changes in geomorphology and drainage that have occurred over the last few million years. Perhaps the most important of these changes are those associated with the progressive capture of the Upper Zambezi tributaries by the young Middle Zambezi River.

Almost half of the basin is covered by various types of miombo woodland, while grasslands and wetlands cover only a small area. Species diversity in the basin is still not fully understood or described, but there are estimated to be around 6-7000 species of flowering plants, 200 species of mammals, 700 species of birds, 290 species of reptile and amphibians, 165 species of freshwater fish (excluding about 500 endemic species in Lake Malawi), 210 species of dragonflies, 1100 species of butterflies and 100 species of freshwater molluscs. The levels and patterns of diversity of other invertebrate groups are very poorly known.

From a continental perspective, there are four significant areas of especial biodiversity conservation interest situated within the Zambezi Basin. These are Lake Malawi; the swamps, floodplains and woodlands of the palaeo-Upper Zambezi in Zambia and northern Botswana; the Middle Zambezi Valley in northern Zimbabwe and the Luangwa Valley in eastern Zambia; and the Gorongosa/Cheringoma/Zambezi Delta area of central Mozambique. There are numerous threats to these ecosystems, among which are land clearance for agriculture, construction of dams and the introduction of exotic species.

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