Eastern Usambara Mountains

The East Usambara mountains are part of the Eastern Arc mountain range of south east Kenya and eastern Tanzania. Forests on the Eastern Arc are regarded as one of the top bio-diversity hotspots in the world on the basis of the high numbers of species endemic to the range. Eastern Arc forests have a unique biota because:

- the forests are at least 30 million years old.
- the forest species have been evolving in isolation from the west and central African forests for at least 10 million years.
- the forests may have acted as a refuge for species lost from southern African subtropical rain forest during climatic changes at close of Tertiary 10 million years ago.
- the forests may have acted as a refuge for species lost from other tropical African forests during
- Pleistocene climatic changes during the last 2.3 million years.
- the remarkable climatic and geological history has resulted in both the survival of ancient evolutionary lineages, and speciation and differentiation.
- the only other comparable areas of high diversity and endemism in tropical African forests are in Cameroon and Gabon, and eastern Zaire.

The East Usambaras are particularly important among the Eastern Arc mountains for a number of reasons. Firstly, they are close to the Indian Ocean and so have a constant humid climate that has encouraged the growth and maintenance of tropical moist forest over very long periods of time.
Secondly, the Amani plateau in the East Usambaras is at the elevation occupied by the particularly species rich sub-montane forest type. Elsewhere in the Eastern Arc, sub-montane forest tends to be a narrow band on the slopes of steep high mountains.
Thirdly, there was until recently substantial areas of relatively undisturbed forest on the East Usambaras. Even though the forests have been heavily disturbed in the last 20 years and the forest area reduced, there are still fine stands of natural vegetation rich in globally rare species of plant and animal.
The Eastern Arc itself is defined on the basis of plant species distributions, which can be related to geological and climatic history. The Arc covers ancient crystalline mountains under the direct climatic influence of the Indian Ocean from the Taita Hills to the Makambako Gap in the southern Udzungwa mountains.
Rainfall and elevation are the main factors affecting dominance and ranges of tree species. There are more endemic taxa in areas of higher rainfall, though a high level of endemism characterizes the Eastern Arc throughout its elevational and latitudinal range. Where the rainfall is more seasonal, the forest tends to be dominated by a few, widespread tree species.
Broad forest types which can be recognized in the Eastern Arc are given below, together with some characteristics and a selection of some of the different names used for each forest type. In the East Usambara mountains the main forest types are Montane Forest, Sub-montane Forest, Lowland Forest, and Dry Lowland Forest. The forests within Amani Nature Reserve are mainly Sub-montane and Lowland.

DRY MONTANE FOREST
Altitude: 1500 m. Rainfall: 1000–1200 mm/year. Synonyms: Montane forest belt, Montane forest, Upland dry evergreen forest, Undifferentiated Afromontane Forest, Dry transitional montane forest. Canopy height: 10–20 (30) m. Basal area: 20–40 m^2/ha. Stem sizes: few large trees 100 cm dbh, most trees <40 cm dbh. Stem density: 240 stems 20 cm dbh/ha.

UPPER MONTANE FOREST
Altitude: 1800 m. Rainfall: 1200 mm/year. Synonyms: Montane forest belt. Bamboo zone. Moist montane forest. Submontane moist forest. Montane forest. Upland rain forest. Montane mossy forest. Undifferentiated Afromontane Forest. Afromontane Bamboo. Afromontane evergreen bush land and thicket. Canopy height: 10–20 m, emergents to 25 m. Basal area: 30–70 m^2/ha. Stem sizes: few large trees 100 cm dbh, most trees <40 cm dbh. Stem density: 330 stems 20 cm dbh/ha.

MONTANE FOREST
Altitude: 1200–1800 m. Rainfall: 1200 mm/year. Synonyms: Montane forest zone. Moist montane forest. Submontane moist forests. Upland rain forest. Montane evergreen forest. Afromontane rain forest. Canopy: 25–40 m., emergents to 50 m. Basal area: 30–120 m^2/ha, usually 50–70 m^2/ha. Stem sizes: many large trees 50 cm dbh, with quite many 100 cm. Stem density: 200–300 stems 20 cm dbh/ha.

SUBMONTANE FOREST

Altitude: 800–1400 m. Rainfall: 1500 mm/year. Synonyms: Moist forest. Submontane moist forest. Lowland rain forest. Submontane rain forest. Zanzibar-Inhambane Transitional Rain forest. Canopy: 25–40 m, emergents to 50 m. Basal area: 30–70 m^2/ha. Stem sizes: many large trees 50 cm dbh with quite many 100 cm. Stem densities: 150–200 stems 20 cm dbh/ha.

LOWLAND FOREST

Altitude: <800 m. Rainfall: 1500 mm/year. Synonyms: Moist forest. Lowland moist forest. Lowland rain forest. Lowland semi-evergreen and evergreen rain forest. Zanzibar-Inhambane lowland rain forest. Canopy: 25–40 m with emergents to 50 m. Basal area: 20–50 m^2/ha. Stem sizes: many large trees 50 cm with quite many 100 cm. Stem densities: 140 stems 20 cm dbh/ha.

DRY LOWLAND FOREST

Altitude: <800 m. Rainfall: 1000–1500 mm/year. Synonyms: Dry evergreen forest. Lowland dry evergreen forest. Lowland dry evergreen forest. Zanzibar-Inhambane undifferentiated forest. Canopy: 15–20 m with emergents to 35 m.

Background to the Eastern Arc

The Eastern Arc mountains are nationally and internationally recognized as being of exceptional bio-diversity value. More than 25 % of the plant species are endemic, with endemism in other groups such as millipedes being far higher. The aim of this section is to put the Eastern Arc into context and explain the reasons for its high bio-diversity values by briefly reviewing: the origin of the term Eastern Arc; topography and geology in relation to the Eastern Arc; present climate and climatic history.

Topography and Geology

Moist forest in Tanzania occurs on three main geological formations: Precambrian crystalline rocks, Cretaceous and Jurassic sedimentary rocks and Tertiary to recent volcanic rocks. The Precambrian rocks are metamorphosed granites, sandstones, shales and limestones formed more than 450 Myr before present (BP). The Cretaceous (*c.* 135 Myr BP) and Jurassic (*c.* 180 Myr BP) sedimentary rocks result from the onset of marine conditions following the break-up of Gondwanaland and development of the Indian Ocean (see below).

The oldest Kilimanjaro lavas are comparatively young, dating from only 1.0 Myr BP with eruptions continuing until the last 10,000 years. The last eruption from Mt. Meru occurred around 1877 AD. The oldest lavas of the southern volcanics at the northern end of Lake Nyasa date from the late Pliocene (5–2.5 Myr BP) with the main activity occurring in the Pleistocene (up to 2 Myr BP). The most recent eruption from Kiejo is thought to have taken place about 1800 AD.

In marked contrast to the geologically recent age of most of the Tanzanian volcanic rocks, the Eastern Arc mountains were formed by block-faulting of Precambrian crystalline rocks starting 290–180 Myr BP. Continuing cycles of erosion and uplift and a reactivation of the faults created the modern mountains during the last 7 million years. Metamorphosed limestone rocks are found along the eastern edge of the Arc where the coastal sediments meet the crystalline mountains.

The wetter eastern side of the Eastern Arc rises sharply out of the coastal plain at around 200 – 500 m elevation. The drier western side either falls sharply (for example the Pare, Usambara and Uluguru); or slopes more gently (as in the Udzungwas) to 500 – 1000 m before the land rises again to the Central Plateau to around 1000 – 1500 m.

Climate

Tanzania is a predominately dry country with nearly half the land area receiving less than 750 mm of rain a year in four years out of five (reliable rainfall), and only 4% of the country receiving over 1250 mm of reliable annual rain. Moist forest occurs in areas where mean annual rainfall exceeds 1200 – 1500 mm and where the dry season is not too marked or enhanced by high temperatures. Rainfall is principally determined by the inter-tropical convergence zone, and modified by topography and the great Lakes of Victoria, Tanganyika, and Nyasa.

The Eastern Arc mountains act as condensers of moisture originating in the Indian Ocean and are important catchment areas in a mainly semi-arid country. Proximity to the Indian Ocean affects rainfall which is higher on those mountains nearer to the coast. Rain shadows cast by the offshore islands of Pemba, Zanzibar, and Mafia also affect rainfall on the mainland. Temperatures are ameliorated by the Indian Ocean, being higher further inland away from the coast.

Annual variation in climate is determined by the Indian Ocean monsoon. The hottest time of year is from December to March when winds are from the north (called the *kaskazi* in Kiswahili). The rainy season peaks in April (*masika*). Southerly winds are from May to October (*kusi*) with the coolest and driest time of year in June and July (*kipupwe*).

The southern monsoon slackens in September (*demani*) with lesser rains in November (*mvuli*). The north-east trade wind brings rain to the East Usambaras and the northern part of the Eastern Arc which have a bimodal rainfall distribution with peaks in November and April. The south-east trade wind brings rain to the southern part with a single rainfall peak. Eastern Arc mountains closer to the coast, such as the East Usambara, or where there is no high ground between them and the coast, such as the Ulugurus, receive the highest rainfall. This is commonly in excess of 2000 mm/year with records exceeding 3000 mm/yr.
On the East Usambara mountains and eastern Ulugurus there is an almost constantly humid climate with no marked dry season and more than 100 mm of rain received in all months of the year. Similar climates may occur in other parts of the Eastern Arc on the upper eastern escarpment edge, but there is a lack of long term data. Rainfall falls sharply west of the escarpment edge to less than 500 mm/year in the western rain shadows. Mist and cloud appears to play an important role in maintaining forest and dry season stream flow on higher mountains west of the escarpment which have a lower orographic rainfall than forests to the east. On the eastern escarpment edge epiphytes are known to be important as interceptors of atmospheric moisture.
Temperature varies with both altitude and geography. The hottest time of year varies in different parts of Tanzania, with the warmest months being February to march in the north-east, November to December in the south-central areas, September to October in central-western areas and February in western Lake Victoria. Mean temperatures fall at a rate of about 0.6 ºC for every hundred meters of elevation ascended. Forest cover is important in maintaining a cooler microclimate. When the forest is removed, soil surface temperatures are much increased.

Climatic and geological history
It is important to know the eastern African climatic and geological history in order to understand the great age and isolation of the Eastern Arc forests. It this combination of age and isolation that has led to their remarkable endemism and biodiversity. The main points are:

- The rifts which give rise to the Eastern Arc mountains date from the break-up of Gondwanaland, 100 Myr BP.
- The forests are probably more than 30 million years old and have been isolated from direct contact with the main west and central African forest block for at least 10 million years following uplift of the Central African Plateau.
- During the Pleistocene (the last 2.3 Myr) there have been about 20 dry periods in Africa. However, stable temperatures of the Indian Ocean off the eastern African coast during these climatic fluctuations maintained high rainfall on the Eastern Arc and so enabled the forests to survive periods of aridity.

The climatic history of eastern Africa can conveniently be divided into three time periods: 1) the break up of Gondwanaland about 100 Myr BP and the tectonic events following it; 2) uplift of the Central African Plateau during the Miocene; and 3) global climatic fluctuations of the last 2.3 million years during the Pleistocene.

Break up of Gondwanaland

In the Triassic to early Cretaceous (*c.* 230–100 Myr BP) Africa was in the center of the Gondwana supercontinent south of its present position, flanked by South America to the west, and India and Antarctica to the east. At this time much of central and eastern Africa must have been arid. From the mid-Cretaceous onwards Gondwana began to drift apart so that by the beginning of the Tertiary (65 Myr BP) oceanic currents flowed around Africa. Africa was 15–18 degrees south of its present position so the inter-tropical convergence zone would have been over the present day Sahara.
Fossil evidence from the late Cretaceous to early Tertiary indicates that north Africa was covered in moist forest about 60 Myr BP. At the break-up of Gondwana rifting was taking place in east and south-east Africa. This suggests that progenitors of the Eastern Arc mountains were formed about 100 Myr BP. After 60 Myr BP Africa moved northwards, completing its union with Eurasia in the middle Miocene 17–18 Myr BP. As Africa moved north the inter-tropical convergence zone would have been over relatively more southern parts of the continent, with tropical forests following it. The Eastern Arc area would have received tropical rainfall by about 30 Myr BP.

Uplift of the Central African Plateau

During the middle Tertiary the ancient peneplaned surface of the Central African Plateau was flexed and warped. In the early Miocene the continental watershed was slightly east of its present position. Around 10 Myr BP, at the end of the Miocene, further uplift raised the Central Plateau to its present level and major rifts developed. The uplift would have created a major barrier between west and central African forests from those on the Eastern Arc and eastern African coast.
From the early Pliocene (about 9 Myr BP) Africa's climatic history becomes clearer. From the beginning of the

Pliocene to mid-Pliocene (6.4 Myr BP) the climate was warm and humid in tropical and north eastern Africa. Off the south-west African coast, strong, persistent up-welling of cold waters began in the late Miocene about 10 Myr BP. After 5 Myr BP a major ice-sheet developed on Antarctica strengthening the cold current, bringing further aridity to south-west Africa. Fossil evidence indicates that there was a major loss of subtropical rain forest taxa in southern Africa at the close of the Tertiary (2.3 Myr BP).

Pleistocene climatic fluctuations

There have been 21 glacials or near glacial periods since 2.3 Myr BP which correspond to dry and cold periods in Africa. During the most recent glacial maximum, about 18,000 years BP, there was a major decrease in rainfall in Africa. Equatorial Atlantic surface temperatures decreased by 4–5 ºC with a greater reduction off north-west and south west Africa. Reduced rainfall coming from the Atlantic climatic system meant that Lake Victoria was almost non-existent around 14,000 BP. In contrast, Indian Ocean surface temperatures just off the tropical east African coast were about the same as at present, so rainfall during the last glacial maximum would have been similar to the present. It is possible that during the last glacial maximum the area of tropical and subtropical rainforest was substantially decreased with remnants only in Cameroon and Gabon; eastern Zaire; and on the Eastern Arc and tropical East African coast.

Summary

The combination of relatively stable geology and climate over very long periods of time is the key to understanding the unique nature of the Eastern Arc vegetation and flora. Diversity in the Eastern Arc flora appears to result from both an accumulation of taxa by long distance dispersal and the survival of biogeographic relicts. Some East Usambara trees are particularly isolated taxonomically, for example the nearest relatives to *Cephalosphaera usambarensis* (Myristicaceae) are on Madagascar and it seems likely that this distribution pattern predates the break-up of Gondwana. Many of the East Usambara trees are Eastern Arc endemics with their nearest relatives in west and central African, for example *Allanblackia stulhmannii* (Clusiaceae), *Polyceratocarpus scheffleri* (Annonaceae), and *Pterocarpus mildbraedii* subsp. *usambarensis* (Fabaceae). Presumably these species represent distribution patterns that predate the uplift of the central African plateau. Long term local climatic and geological stability clearly enables these isolated taxa to survive historical global climatic fluctuations.

Moreover, the fact that so many Eastern Arc plants have differentiated from their parental taxa, suggest that the unique Eastern Arc environment also promotes speciation. Hence it is a center of evolution as well as a center of diversity.