

# The phytogeography of moist forests across Eastern Zimbabwe

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**Background and aims** – During the 1970s, a comprehensive survey of moist forest areas across Zimbabwe's Eastern Highlands was carried out, from Nyanga in the north to Chirinda Forest in the south. All tree stems 8 cm diameter or greater in both canopy and sub-canopy layers were measured in 176 quarter-hectare plots, and plots were then classified into 12 altitude-related forest types. The aim of the present study is to categorise the woody species recorded in these plots in terms of their chorological status. The findings are compared to similar analyses from moist forests across Malawi.

**Material and methods** – All tree species recorded during the initial survey were listed and placed into 12 described chorological (phytogeographical) categories based on their continental distribution. Their occurrence across the 12 previously described forest types is given.

**Key results and conclusions** – A total of 211 tree species was recorded from 176 plots. Most species (86, or 40.8%) are Afromontane endemics or near-endemics, while 48 species (22.7%) are Guineo-Congolian linking, 31 (14.7%) are Eastern endemic or near-endemics, and 16 (7.6%) are sub-Afromontane endemics or near-endemics. The remainder comprise African linking and Zambebian species. This shows that species of the moist forests of eastern Zimbabwe form a complex phytogeographical mix. While Afromontane species dominate at high altitudes, Guineo-Congolian and Eastern species become more common at lower altitudes. In terms of proportions of chorological categories, results were found to be similar to those from forest studies in Malawi.

**Keywords** – Altitude; Malawi; moist forest; phytogeography; Zimbabwe.

## INTRODUCTION

Globally there has been much interest in tropical moist forests (often termed rain forests), including on the importance of their relatively high species diversity, the numbers of species of restricted distribution found there, and in moist forests being a habitat of conservation significance (e.g. Sayer et al. 1992; Burgess et al. 2004). In Africa, moist tropical forests comprise a wide range of species, with differing geographical distributions. Some are mostly confined to lowland areas while others are restricted to higher altitudes. As White (1978, 1983a) has noted, many woody forest species have relatively wide distributions, whether across the Congo Basin into West Africa, along the chain of mountains on the

eastern side of the continent from Ethiopia to South Africa, or confined to lower-altitude areas closer to the Indian Ocean coastline. Especially in eastern and southern Africa, where many of the moist forest areas are scattered and associated with mountains or higher ground, it is not clear how unique each of these various areas are in terms of their species composition – whether each forest patch comprises a fortuitous association of species of differing geographical origin, or whether there is a more consistent or repeating set of species associations and ecologically coherent communities. Another important question is whether these associations change with latitude, altitude, or with substrate (Müller 1999). In addition, it would be interesting to

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*Plant Ecology and Evolution* is published by Meise Botanic Garden and Royal Botanical Society of Belgium  
ISSN: 2032-3913 (print) – 2032-3921 (online)

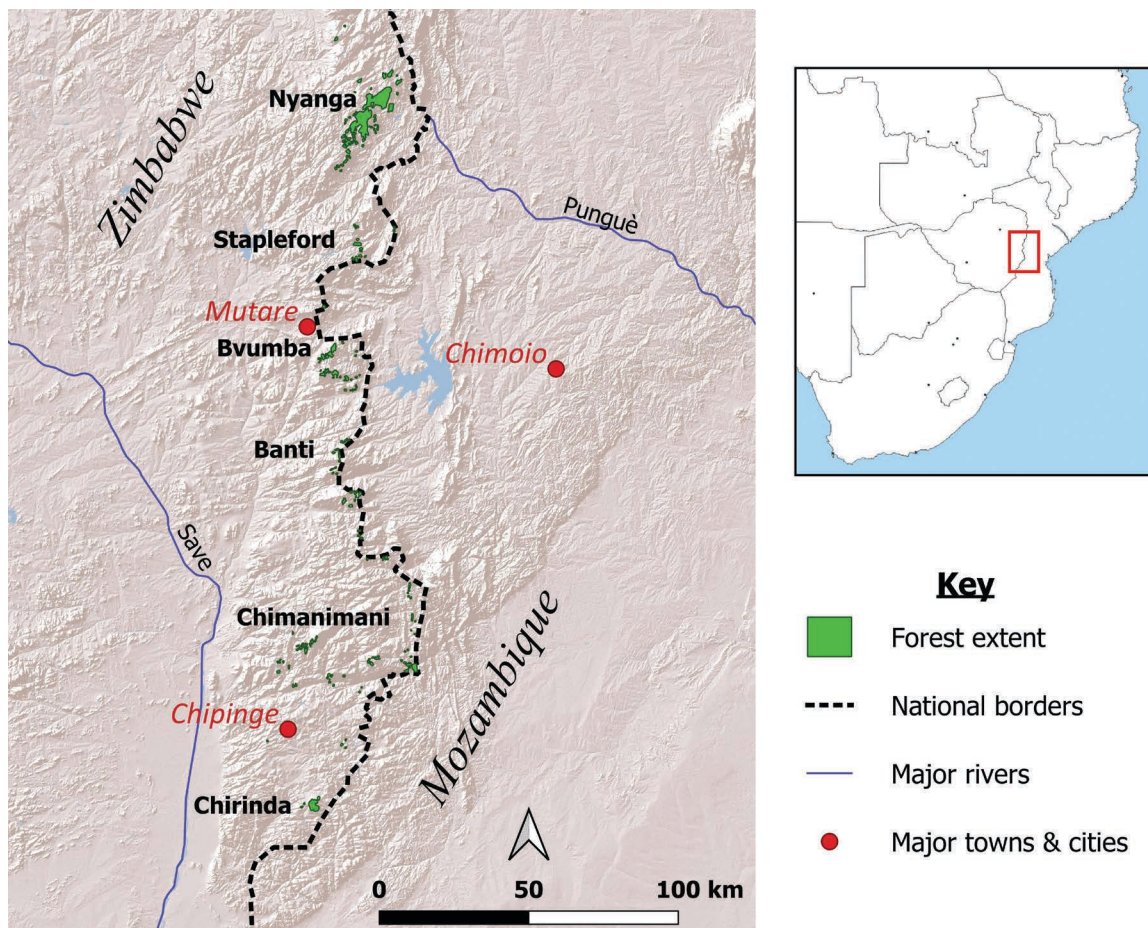
understand what the distributional and evolutionary origins of moist forest species might be, and if they are similar to each other or quite varied across the region.

In the 1970s, one of the present authors, Tom Müller, undertook a wide-ranging study of what were considered to be the remaining areas of tropical moist forest across the Eastern Highlands of Zimbabwe (Müller 1999, 2006). The main objectives of this study were to try and determine the range and distribution of forest types, their species composition, and to see which readily measurable environmental factors (e.g. altitude, aspect, slope, soil type) might determine this. The study systematically recorded all tree species with stems  $\geq 8$  cm diameter within 176 quarter-hectare plots. These plots spanned the full geographical and altitudinal range of forest in the country, with plots recorded from all larger forest patches. The 8 cm diameter limit was chosen to conform to locally accepted forestry practice at that time, and because the use of a lower diameter limit would have been far more time consuming. A summary of the distribution and extent of the 12 forest types identified has been produced (Müller 1999, 2006) but, apart from data on limited forest loss over the last 50 years (Timberlake & Müller 2021), no other quantitative findings have yet been published.

Given the availability of this dataset, the opportunity was taken to list all recorded tree species from the plots and allocate each to one of White's phytochoria or biogeographical units (see below). This was done to provide a reference source for future studies on the phytogeography of south-central African forests, and also to help determine what the broad affiliations for Zimbabwe's forests might be. A later paper will look at the relative proportions of each species in terms of its basal area across the 12 forest types; an initial attempt at doing this using a subset of data was presented at an AETFAT Congress in 2007 (Timberlake & Müller 2007). To date, the only other detailed study on the phytogeography of south-central Africa's moist forests is that by Dowsett-Lemaire (1988a, 1989, 1990) and White et al. (2001) for the forests of Malawi. Results of the Zimbabwe phytogeographical analysis are discussed and compared to this study.

### STUDY AREA

Moist forests are localised in Zimbabwe, being found principally on the windward slopes of a 250 km stretch of mountains along the Zimbabwe-Mozambique borderlands of Manicaland Province from 17°44'S to 20°32'S (fig. 1). These east- and south-east-facing slopes intercept moisture-



**Figure 1** – Distribution of moist forest areas across eastern Zimbabwe. Map created with QGIS v.3.14.16-Pi (QGIS Development Team 2017). Imagery: Esri World Shaded Relief (© Esri, all rights reserved; [https://server.arcgisonline.com/ArcGIS/rest/services/World\\_Shaded\\_Relief/MapServer](https://server.arcgisonline.com/ArcGIS/rest/services/World_Shaded_Relief/MapServer)).

**Table 1** – Forest types in eastern Zimbabwe, including extent, number of plots and species recorded, and mean basal area (based on Müller 1999 and fieldsheets).

Forest type	Zone	Area (ha)	# plots recorded	# species recorded	Mean basal area (m <sup>2</sup> /ha)
1. <i>Syzygium chimanimaniense</i> montane forest		655	12	48	46.1
2. <i>Afrocrania volkensii</i> montane forest		375	8	46	45.8
3. <i>Widdringtonia nodiflora</i> forest		40	0	n/a	n/a
4. <i>Ilex mitis</i> – <i>Schefflera umbellifera</i> – <i>Maesa lanceolata</i> montane forest	Upper Montane (~1650–2100 m)	695	15	69	48.5
5. <i>Syzygium guineense</i> subsp. <i>afromontanum</i> montane forest		2420	26	90	44.4
6. Regenerating montane forest		1935	13	72	39.0
7. Mixed sub-montane forest		2130	25	110	42.7
8. <i>Craibia brevicaudata</i> forest	Sub-Montane (~1350–1650 m)	35	4	48	49.9
9. <i>Albizia</i> -dominated regenerating forest		380	5	46	43.8
10. <i>Albizia schimperiana</i> forest		110	6	58	51.5
11. Medium altitude forest	Medium altitude (~850–1350 m)	1370	35	127	46.6
12. Lowland forest	Low altitude (~320–850 m)	490	27	91	35.4
<b>Total</b>		<b>10,635</b>	<b>176</b>	<b>211</b>	<b>43.7 (mean)</b>

bearing air flows from the Mozambique Channel, air flows that provide additional moisture during the long dry season. The forests range in altitude from 320 m to 2100 m and have a very disjunct distribution. They range greatly in size, many being patches of a few hectares, but can be blocks of up to a few square kilometres (Müller 2006); the largest patch at 2850 ha (28.5 km<sup>2</sup>) is found on the slopes on Mt Nyangani.

There are four main centres of forest development (fig. 1), which are (from north to south) the Nyanga mountains (Clark et al. 2017), the area around Stapleford Forest and the Bvumba mountains (Timberlake et al. 2020) including Banti, the mountains and uplands of Chimanimani District (Timberlake et al. 2016; Wursten et al. 2017), and finally the southern outlier of Chirinda Forest (Timberlake & Shaw 1994). Total forest extent is estimated at approximately 107 km<sup>2</sup> (Müller 2006), less than 0.03% of the country's total area.

Average annual rainfall across forest areas is at least 1200 mm, most falling in the warmer rainy season but with significant precipitation in the form of rain and mist from low clouds during the cooler dry season; this greatly reduces the physiological stress of the long dry season. The main environmental variables thought to control species distribution and the species composition of the 12 forest types (see table 1) are altitude (often a proxy for mean temperatures), amount of available moisture (especially during the dry season), past human disturbance and, to a lesser extent, soil type, aspect, and topography (Müller 1999).

Although there has been little previous work on their distribution and composition, the importance of these moist forests in terms of biodiversity has been widely recognised in Zimbabwe (e.g. Wild 1968 for plants; Pinhey 1978 for Odonata; Poynton & Broadley 1978 for reptiles and amphibians; Irwin 1981 for birds).

## PHYTOGEOGRAPHICAL CONCEPTS

Unlike Keay (1959) and earlier workers, who based phytogeographical units on the distribution of genera and families, White (1976, 1983a) proposed a new chorological classification of African vegetation based on the patterns of distribution shown by species. He thus defined 18 main phytochoria, which, according to levels of endemism and species richness, are divided into three categories: Regional Centres of Endemism, Regional Transition Zones, and Regional Mosaics.

A Regional Centre of Endemism has more than 50% of its vascular plant species confined to it and a total of more than 1000 endemic species (White 1983a). There are nine such regions in Africa, of which two concern Zimbabwe – the Zambezi region and the archipelago-like Afromontane region. Zimbabwe lies entirely within the Zambezi region: it is one of the richest regions in terms of species diversity, but the main vegetation types are different forms of woodland and thicket, hence the region is unlikely to be more than very poorly represented in the country's moist forests.

Within the Zambezi region sit enclaves of the Afromontane archipelago-like region, as shown in White's map (White 1983a). In contrast to the widespread but poorly represented Zambezi species, Afromontane endemics are expected to be important elements in the upland forests of eastern Zimbabwe. A small subset of Afromontane affinity included here, the sub-Afromontane element, applies to species associated with montane vegetation but occurring overall at a lower elevation than Afromontane endemics.

Regional Transition Zones and Regional Mosaics have fewer than 50% endemism and are transitional in various ways (White 1983a). Among Regional Mosaics, White (1983a) recognised two such regions of Eastern (coastal) elements, from north to south the Zanzibar-Inhambane and



Tongaland-Pondoland regions. During the preparation of the Evergreen Forest Flora of Malawi in the 1980s (published as White et al. 2001), this concept had to change to include a wider region of Eastern endemism, containing both of those coastal mosaics with an extension inland, from now on termed the Eastern region. Geographically, it comes west to the fringes of the Lake Victoria basin and the eastern half of the Zambezi region (Dowsett-Lemaire 1988a: 83; White et al. 2001: 16). The main vegetation types of the Eastern region are evergreen moist forest and related types and there is thus virtually no overlap with Zambezi or other drier vegetation. As with the Afromontane region, the Eastern (forest) region has a discontinuous, archipelago-like distribution with islands of vegetation scattered over a large area dominated by other regions; except for the coastal belt these islands are too small to be mapped. The proportion of endemic elements is less than 50% overall and decreases from east to west.

In addition to species endemic to one of these regions, the forests of Zimbabwe also consist of species of wider distribution belonging to two or more phytochoria, termed 'linking species'. Species of wide distribution found in three or more phytochoria are termed African linking. Some of these linking elements are also ecological transgressors, occurring in more than one vegetation type. The most important category of linking species found in moist forest usually consists of Guineo-Congolian linking elements, i.e. species that are characteristic of Guineo-Congolian forest vegetation (including secondary forest) and which also occur in other forest types on the continent. In contrast, African linking species refer to taxa not represented in the Guineo-Congolian region, or only on its margins. The distinction between a Guineo-Congolian linking and an African linking taxon is sometimes difficult to establish: examples include *Albizia glaberrima* and *Diospyros abyssinica* subsp. *abyssinica* which are found in the drier forest types at the periphery of the Guineo-Congolian region, but also locally in semi-evergreen moist forest further inside this region. For the moment they are still classified as African linking but that decision could be reversed. The status of a few species classified by White et al. (2001) in one or other category has had to change in light of improved knowledge of their distribution and ecology (e.g. in Hawthorne & Jongkind 2006; William Hawthorne, University of Oxford, in litt.): thus *Antidesma membranaceum*, *Bridelia micrantha*, *Margaritaria discoidea*, and *Psyrax parviflora* are here changed from African linking to Guineo-Congolian linking as these pioneer species occur in secondary forest right in the heart of the Guineo-Congolian region, including the evergreen forest zone. Conversely, *Ficus vallis-choudae* and *Vitex doniana* have been moved from Guineo-Congolian linking to African linking as they are completely absent from Guineo-Congolian vegetation in West Africa and the *Vitex* is marginal at best on the southern fringes, as in southern Congo-Brazzaville.

White (1978) subdivided the Afromontane archipelago into seven subregional groups, based on inter-island distances. These are 'West African' (mostly Cameroon/Nigeria), 'Ethiopian', 'Imatongs-Usambara', 'Kivu-Ruwenzori', 'Uluguru-Mulanje', 'Chimanimani' (= eastern

Zimbabwe and adjacent Mozambique), and 'Drakensberg'. The highlands of Angola were considered too impoverished to be included, but are nevertheless recognised by ornithologists, given a significant level of local endemism of the Angolan scarp (Dowsett 1986). White (1978, 1983a) has repeatedly stressed that, despite the wide intervals between mountains, the endemic montane flora shows a remarkable uniformity. He has also shown (White 1981, 1983b) that some Afromontane near-endemic trees – presumably more tolerant of climatic variations than stenotopic species – have satellite populations in mid-altitude forests in south-central Africa (on the Congo-Zambezi watershed) and in some upland areas of Congo-Brazzaville, Gabon, and Cameroon, indicating a possible linking route between the mountain floras of eastern and western Africa in relatively recent times.

The different chorological categories used in this analysis are listed below (see table 2). Not all species defined as belonging to a particular region are strict endemics (that is, strictly confined to a region): species belonging overwhelmingly to one region but also feebly represented elsewhere – either in neighbouring transition zones or in more distant satellite populations – are referred to as 'near-endemics' in the meaning of White (1979). Some Afromontane 'endemics' may occur marginally beyond the African continent, as in south-west Arabia or Madagascar, but they are still classified as endemics because we are concerned with a comparison of lowland and montane elements in an African context. If this is not done the terminology becomes too complicated and the situation in Africa becomes blurred.

## METHODS

Over 200 georeferenced plots, each 0.25 ha (most being 50 × 50 m) and marked on aerial photos, were recorded during Müller's study in the 1970s. Of these, 176 plots have data on all tree stems larger than 8 cm dbh, by species, and were used in this paper. Although lianas were recorded, diameter measurements were not made and hence these species are not incorporated here. Altitude, slope, soil type, and other ecological aspects such as disturbance, were also recorded (Müller 2006). Additional information recorded (although not used in this paper) included species composition and cover-abundance in both sapling and ground layers. Where there was uncertainty as to species identity, a voucher specimen was collected. These were later identified (most by Tom Müller and Bob Drummond) at the National Herbarium in Harare (SRGH), although only a small number were ever formally accessioned. Species authorities are given in full in supplementary file 1.

Data from all 176 quarter-hectare plots were put into Excel spreadsheets from the original summary fieldsheets, with the total number of measured stems noted for each plot by species. Basal area was calculated from diameter or circumference (field data came in both formats at various times) using standard formulae. Any stems less than 8 cm dbh (or the equivalent circumference of 25 cm) were omitted. Plots were then grouped under each of Müller's forest types (Müller 1999 and unpublished notes, table 1) and total basal area was calculated for each type. Comparable forest plot data were not available for Malawi. As no plots were

**Table 2** – Phytogeographical affinities of moist forest species based on recorded stems in Zimbabwe plots (Müller 2006) and equivalent percentages for Malawi forests (from White et al. 2001: 50). Note: ‘Uncertain’ species were excluded just for Malawi as there were too many and total figures would be distorted.

Chorological category	# spp.	%	% for Malawi forests
African linking species (incl. Afromontane/Zambeziian linking)	17	8.0	15.0
Afromontane endemic/near-endemic species	86	40.8	43.0
Sub-Afromontane endemic/near-endemic species	16	7.6	4.6
Eastern endemic/near-endemic species	31	14.7	15.5
Guineo-Congolian linking species (incl. Guineo-Congolian/Afromontane linking)	48	22.7	17.8
Zambeziian endemic/near-endemic species	12	5.7	4.1
Uncertain	1	0.5	n/a
<b>Total</b>	<b>211</b>	<b>100</b>	<b>100</b>

recorded for the distinctive *Widdringtonia nodiflora* forest (type 3), this type was omitted from some of our results.

For each forest type, the component species were allocated to a chorological unit based primarily on those given in White et al. (2001), with White (1983a) and Friis (1992) being used where a species was not found in Malawi. Some small changes concerning Guineo-Congolian and African linking species are detailed above under definitions of chorological categories. Any species still lacking a chorological unit were assessed by us using mapped distribution data available on the African Plants Database (2020). The 12 categories recognised (plus uncertain) are listed and grouped in table 2.

Species nomenclature and family arrangement follow those used in the Flora of Zimbabwe website (<https://www.zimbabweflora.co.zw/>, Hyde et al. 2020) with some minor modifications, and many have been significantly updated from the names used during the original survey. Where appropriate, the species name under which it was originally recorded during the surveys is also given.

These summary data were then amalgamated into a single table (supplementary file 1) listing all forest species alphabetically by genus and species, indicating the lifeform (e.g. canopy tree, understory tree), chorological unit, total number of plots in which the species occurred, and the presence of a species within each forest type. In order to indicate which species were more significant, those that contributed 1% or more to the total basal area recorded for each type are indicated (X); the remainder (indicated by O) being relatively minor in this regard.

## RESULTS

The number of plots recorded for each of Müller’s forest types, the number of species in each and the mean basal area are shown in table 1. From this it can be seen that the coverage in terms of number of plots for each type was not even, and that total species number per type was also not uniform. Apart from the obvious lack of plots in type 3, sampling density ranged from around one plot per 8.8 ha for type 8 to one plot per 93 ha and per 149 ha for types 5 and 6, respectively. Medium altitude forest (type 11) was the most species-rich, although also with the largest number of plots

recorded, while the highest altitude forest types (types 1, 2), regenerating forest (type 9) and *Craibia brevicaudata* forest (type 8) were the least species-rich. Basal area did not differ greatly across types with a mean of 43.7 m<sup>2</sup>/ha, although lowland forest (type 12) was surprisingly low in this regard at 35.4 m<sup>2</sup>/ha.

Although 35 species were present in only one plot, three species (*Aphloia theiformis*, *Macaranga mellifera*, and *Xymalos monospora*) were present in 100 or more plots (supplementary file 1). Skewness of species distribution is also shown by only 72 (34%) species being found in more than 10% (18) of total recorded plots.

Not surprisingly, the main chorological category of Zimbabwe’s moist forest tree species comprises Afromontane (near-)endemic species with 86 species, and when 16 sub-Afromontane elements are added to the total, these constitute nearly half (48.4%) of the floristic composition (table 2, fig. 2). The Guineo-Congolian linking category with 48 species comes next (including two Guineo-Congolian/Afromontane linking species) and, together with Afromontane and sub-Afromontane species, these comprise 71.1% of the total. There are also 31 Eastern (near-)endemic species.

### Afromontane (near-)endemic species

Of the 86 Afromontane species, a few are endemic only to the Chimanimani montane group: *Faurea rubrifolia*, *Maytenus chasei*, *Pavetta umtalensis*, and *Canthium oligocarpum* subsp. *angustifolium* (the species as a whole being present in five montane subregions). A few more Afromontane (near-)endemics are confined to the Chimanimani and Drakensberg groups: *Cassinopsis ilicifolia*, *Chionanthus foveolatus*, *Curtisia dentata*, *Dovyalis lucida*, *Eleaodendron croceum*, *Psydrax obovata*, *Searsia tumulicola*, *Trimeria grandifolia*, and *Zanthoxylum davyi*. But the majority are more widespread, being present in three or more subregional groups. At the other end, the following species occur in all seven montane groups: *Apodytes dimidiata*, *Hypericum revolutum*, *Ilex mitis*, *Maesa lanceolata*, *Nuxia congesta*, *Olea capensis*, *Pittosporum viridiflorum*, *Prunus africana*, and *Rapanea melanophloeos*. As many as 16 species occur in six groups: *Albizia gummifera*, *Allophylus abyssinicus*, *Cassipourea gummiflua*, *Catha edulis*, *Cyathea dregei*,

*Dovyalis macrocalyx*, *Halleria lucida*, *Ochna holstii*, *Peddiea africana*, *Podocarpus latifolius*, *Polyscias fulva*, *Schrebera alata*, *Scolopia stolzii*, *S. zeyheri*, *Solanecio mannii*, and *Xymalos monospora*. *Alangium chinense*, not identified in our plots but present in the Eastern Highlands, is also represented in all six groups, being absent only from the Drakensberg subregion. Species present in six of seven groups are missing either from Ethiopia or from West Africa. Several also reach the Angolan highlands (e.g. *Cassipourea gummiflua*, *Ilex mitis*, *Olea capensis*, *Podocarpus latifolius*, *Polyscias fulva*, etc.) although, in some cases, they do not make it to the Cameroon/Nigeria highlands (e.g. *Olinia rochetiana*, which is very close to *O. vanguerioides* and sometimes considered conspecific, and *Syzygium guineense* subsp. *afromontanum*). Indeed, several of the near-endemics are represented in mid-altitude forest patches on the Congo-Zambezi watershed of the Southern Migratory Track (White 1981; White et al. 2001) between the mountains of eastern Africa and the Angolan and Cameroon highlands: *Podocarpus latifolius*, *Rapanea melanophloeos*, and *Nuxia congesta* are good examples. *Polyscias fulva* and *Olea capensis* are extreme examples of Afromontane near-endemics as they occur not only on the Southern Track but also very locally in the tropical lowlands, but they are infinitely more common in, and characteristic of, montane vegetation. Most of these widespread trees produce fruit dispersed by birds, and it may be significant that a key disperser, the Afromontane near-endemic Olive (Rameron) Pigeon *Columba arquatrix* (Dowsett-Lemaire 1988b), undergoes migrations outside the breeding season and is also present in very small numbers along the Southern Track (as in Mwinilunga District in north-western Zambia, Dowsett et al. 2008). There is an almost perfect match between the ranges of Olive Pigeon and *Olea capensis*, one of its most important food plants (Dowsett-Lemaire & Dowsett 1998, 2006: 50). Finally, some of the near-endemics include

species that extend into the Cape region, e.g. *Cassinopsis ilicifolia*, *Cussonia spicata*, *Podocarpus latifolius*, *Rapanea melanophloeos*, and *Widdringtonia nodiflora*.

**Sub-Afromontane (near-)endemic species**

Most of these 16 species occur at medium altitudes. *Newtonia buchananii* is one of the more characteristic trees of this forest type, being locally abundant in forests of central and southern Malawi between 1000 and 1600 m; in Zimbabwe, with increasing latitude this is slightly lower (below 1400 m, cf. forest type 11). Several of the near-endemic species occur locally on the Congo-Zambezi watershed. Among them *Cyathea manniana*, *Newtonia buchananii*, *Suregada procera*, and *Trichilia dregeana* all reach the highlands of Angola; *Newtonia* and *Trichilia* also reach Cameroon and even (*Trichilia*) the uplands of Guinea and Liberia. *Calodendrum capense* is predominantly of Afromontane affinity in the northern part of its range (Uganda and Kenya) but less so from Malawi southwards. By contrast, *Bersama swynnertonii* and *Strychnos mellodora* are endemic to the Chimanimani subregion, whereas *Ochna arborea* and *Vangueria esculenta* extend from Zimbabwe to South Africa. Thus the ‘origins’ or distribution patterns of plants of this category are as varied as for Afromontane species.

**Eastern (near-)endemic species**

The 31 species listed are characteristic of evergreen forest and thicket at low and medium altitudes on the eastern side of the continent, several reaching as far inland as eastern Congo-Kinshasa and one or two have satellite populations in Nigeria or Angola. Some show Afromontane intrusions (i.e. they occasionally reach higher mountains or high altitudes), such as *Ficus scassellatii* and *Gymnosporia mossambicensis*. Only one species, *Synsepalum chimanimani*, is endemic to eastern Zimbabwe and adjacent Mozambique. Although

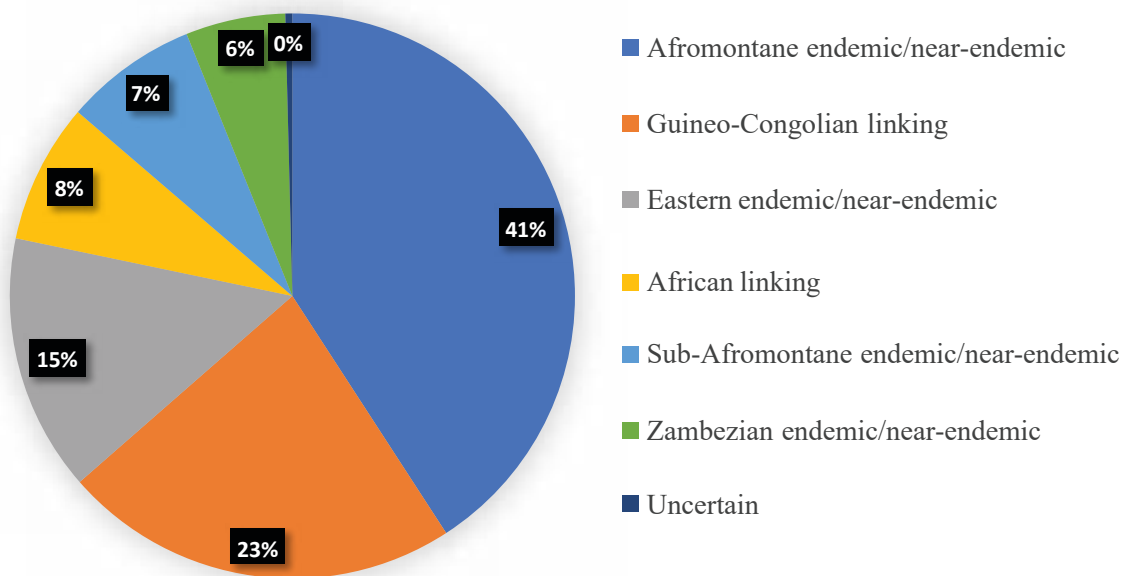


Figure 2 – Chart showing proportions of species of different chorological categories in the Zimbabwe woody moist forest flora.



the type of *Necepsia castaneifolia* is from the north of Madagascar, subsp. *chirindica* is endemic to eastern Zimbabwe. By contrast, several taxa are very widespread, from Ethiopia and/or Somalia south to KwaZulu-Natal or the Eastern Cape (*Drypetes natalensis*, *Macaranga capensis*, *Strychnos mitis*), or south to Zimbabwe and adjacent Mozambique (*Ficus scassellatii*, *Warneckea sansibarica*), whereas others extend from eastern Africa to South Africa (*Chrysophyllum viridifolium*, *Englerophyllum natalense*, *Gymnosporia mossambicensis*, *Tarenna pavettoides*). Several species with wide or more limited distributions on the African continent also occur on islands of the Indian Ocean, e.g. *Rinorea arborea* (from Kenya to southern Mozambique) reaches Madagascar, *Diospyros natalensis* (from eastern Congo-Kinshasa and Kenya to the Eastern Cape) also reaches Madagascar, *Pyrostia bibracteata* (Kenya to Mozambique) also occurs in Seychelles and Madagascar, and *Filicium decipiens* (Ethiopia to Mozambique) even reaches south India and Sri Lanka.

### Zambeian (near-)endemic species

Tree species endemic (or nearly so) to the Zambeian region are normally encountered in woodland and dry thicket, vegetation types drier than evergreen or rain forest. The 12 listed here are rather marginal, with the exception of *Mimusops zeyheri*. *Uapaca lissopyrena* is considered conspecific with *U. guineensis* by White et al. (2001) and the latter is a Guineo-Congolian linking species, normally encountered in swamp or fringing forest.

### Guineo-Congolian linking species

Not surprisingly, the majority of the more widespread species falling outside a regional centre of endemism are to be found in this category, the Guineo-Congolian region being originally dominated by moist forest. These 48 species are found mainly in lowland or mid-altitude forest types, but may ascend into the lower levels of Afromontane forest, even to the highest level in the case of *Clausena anisata*. The majority of Guineo-Congolian linking species found in western or central Africa occur there in drier types of moist forest, especially semi-evergreen (or semi-deciduous, Hawthorne & Jongkind 2006) forest, e.g. *Khaya anthotheca* and *Milicia excelsa*. Such species are often more characteristic of degraded, secondary forest: thus *Albizia adianthifolia* and *Celtis mildbraedii* are important pioneers, but disappear with the closing of the canopy. *Harungana madagascariensis* is one of the most characteristic small trees of the early stages of forest regrowth throughout the Guineo-Congolian region, as are *Bridelia micrantha*, *Ficus exasperata*, *Margaritaria discoidea*, and *Trema orientalis* in secondary forest or on edges. *Xylopia aethiopica* is also an important forest pioneer, being dominant in young forest about 25–30 m tall in some areas (e.g. at Odzala in the north of Congo-Brazzaville, Dowsett-Lemaire 1996: 258) and is an important constituent of swamp forest, as are *X. parviflora* and *Syzygium owariense*. A few species are rather local in western Africa, favouring the cooler climate of hills and plateaux, e.g. *Celtis gomphophylla*, *Rothmannia urcelliformis*, and *Oxyanthus speciosus*. The latter falls into

a narrower category of Guineo-Congolian/Afromontane linking species, together with *Zanthoxylum gilletii* which is found throughout the Guineo-Congolian region in secondary situations.

A few species extend into riparian forest of the Sudanian region to the north of the main forest block, such as *Erythrophleum suaveolens*, *Ficus sur*, *Margaritaria discoidea*, *Shirakiopsis elliptica*, and *Zanha golungensis*. Many extend widely into forest enclaves in other phytochoria, often reaching the coastal belt of eastern Africa (e.g. *Albizia adianthifolia*, *Blighia unijugata*, *Celtis mildbraedii*, *Croton sylvaticus*, *Erythrophleum suaveolens*, *Milicia excelsa*, *Trema orientalis*) while *Trilepisium madagascariense* extends to Madagascar.

### Afromontane/Zambeian linking species

There is only one Afromontane/Zambeian linking species, *Heteromorpha arborescens*, which is common in and characteristic of both the Zambeian and Afromontane regions.

### African linking species

These 17 species occur in three or more phytochoria, and most have a circum-Congo distribution. *Breonadia salicina* is a good example, being characteristic of riparian vegetation from Mali east to Ethiopia, south to KwaZulu-Natal and west to Angola; it also extends to Yemen and Madagascar. Several of these circum-Congo species could marginally be considered Guineo-Congolian linking as they occur in the drier types of Guineo-Congolian forests or at its fringes (e.g. *Diospyros abyssinica* subsp. *abyssinica*). Others are typical only of very dry forest in the Guineo-Congolian region and extend into riparian forest or moist woodland in savanna to the north, e.g. *Ekebergia capensis*, which then ascends to high altitudes on the eastern side of Africa from Ethiopia south to South Africa. This and several other species are ecological transgressors, occurring in more than one vegetation type over a wide range, e.g. *Gymnospora buxifolia* (Ethiopia to the Cape, west to Namibia and Angola). *Mystroxydon aethiopicum* is a versatile ecological transgressor, being characteristic of upland vegetation from Guinea and Cameroon to Ethiopia and south to South Africa, but is also found in riparian forest, woodland and bushland on termite mounds at low altitudes. Moreover, it extends to several Indian Ocean islands, including Madagascar.

## DISCUSSION

It is recognised that plot coverage was not particularly high with a total sampled area of 44 ha or just 0.4% of the total forested area. However, at the time the plots were carefully chosen to represent the full range of forest types and geographical locations. In addition, the number of woody stems measured was 29,100, giving comprehensive coverage. Even though there were no plots recorded for the distinctive *Widdringtonia* forest (type 3) compared to the high number of plots that were recorded for Medium altitude forest (type 11), it is apparent that Mixed sub-montane forest and Medium altitude forest (types 7 and 11, respectively)

were particularly species-rich. As expected, there was a general tendency to greater species richness with decreasing altitude. As plot data were not available for the Malawi study, or for other similar forests in the region, useful comparisons cannot be readily made at this stage.

The proportion of Afromontane species was expected to increase with altitude, and that of 'lowland' species, especially Guineo-Congolian linking species, to decrease. This was clearly shown by Timberlake & Müller (2007) using a subset of basal area data from Müller's Zimbabwe study. They showed that the total basal area comprised of Afromontane elements was around 41 m<sup>2</sup>/ha in Muller's type 1 and type 2 forests, declining to 17 m<sup>2</sup>/ha in Medium altitude forest (type 11), and 0.7 m<sup>2</sup>/ha in Lowland forest (type 12). In contrast, Guineo-Congolian linking elements totalled just 1.3 and 0.1 m<sup>2</sup>/ha in type 1 and type 2 forests, respectively, rising to 10.7 and 11.0 m<sup>2</sup>/ha in type 11 and type 12 forest at lower altitudes.

In Malawi, the proportion of Afromontane species was used to define the three main forest types of the country: thus Afromontane forests are defined as such when they have in excess of 50% Afromontane (near-)endemic species while 'mid-altitude forests' have between 25 and 50% and 'lowland forests' less than 25% (Dowsett-Lemaire 1989, 1990; White et al. 2001: 60–64). On Mount Mulanje, the only large mountain with a near-continuum of forest from low to high altitude (Dowsett-Lemaire 1988a), the proportion of Afromontane elements was found to increase from 22% at 650–950 m to 44% in mid-altitude forest (up to 1350 m) and to 76% in Afromontane forest (1600–1950 m on upper slopes and plateaux). Elsewhere in Malawi, the elevation of mid-altitude forests is somewhat higher as conditions are warmer than on the wet southern slopes of Mount Mulanje; they lie mostly between 1100–1200 m and 1500–1600 m. In Zimbabwe, no attempt was made to define mid-altitude forest using these criteria so a direct comparison is difficult, but Medium altitude forest (Müller's type 11) has just 29% Afromontane elements.

There is a general tendency for montane trees to occur at lower altitudes with increasing latitude and a shift from tropical to temperate conditions. For example, in South Africa and especially in the Cape, *Podocarpus latifolius*, *Olea capensis*, and other montane near-endemic trees occur only a short distance above sea level. Although not specifically looked at here, this phenomenon has also been noted for some individual species distributions between Zimbabwe and Malawi (Françoise Dowsett-Lemaire pers. obs.), and in addition Zimbabwe appears to have a lower diversity of montane forest species than Malawi or Tanzania (cf. Dowsett-Lemaire 1989: 118).

With the proviso that the Malawi study included a wider range of species (with lianas, slender climbers and smaller shrubs), very similar figures were obtained for a sample of 660 species (excluding 24 elements of uncertain taxonomic and chorological status) over an altitudinal range of (500–)600–2500 m (White et al. 2001: 50 and last column in table 2). Thus, we get a similar figure of 47.6% Afromontane elements (including 4.6% of sub-Afromontane (near-)endemics), followed by 17.8% of Guineo-Congolian

linking species and 15.5% of Eastern (near-)endemics. The remainder comprise African linking and Zambebian species.

To conclude, species constituting the evergreen moist forests of eastern Zimbabwe form a very complex phytogeographical mix, ranging from narrow Afromontane endemics to pan-African ecological transgressors. Not surprisingly, the proportions of the different phytochoria represented are very similar to those observed in the Malawi forest flora, and change markedly with altitude. There are few species restricted to these forests (i.e. local endemics), but these include some belonging to the Afromontane region and one Eastern (lowland) species.

#### SUPPLEMENTARY FILES

**Supplementary file 1** – The 211 woody species > 8 cm dbh recorded in 176 forest plots across moist forests of Eastern Zimbabwe, with indications of their life-form and phytogeographical affiliation (pdf).

<https://doi.org/10.5091/plecevo.2021.1814.2453>

**Supplementary file 2** – The 211 woody species > 8 cm dbh recorded in 176 forest plots across moist forests of Eastern Zimbabwe, with indications of their life-form and phytogeographical affiliation (Excel spreadsheet).

<https://doi.org/10.5091/plecevo.2021.1814.2455>

#### ACKNOWLEDGEMENTS

We would like to thank two anonymous referees for suggesting structural improvements to the paper and Thomas Timberlake for drawing fig. 1.

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Communicating editor: Alexandra Ley.

Submission date: 4 Oct. 2020

Acceptance date: 31 Mar. 2021

Publication date: 24 Jun. 2021