Compositional gradients of plant communities in submontane rainforests of Eastern Tanzania

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COMPOSITIONAL GRADIENTS OF PLANT COMMUNITIES IN SUBMONTANE RAINFORESTS OF EASTERN TANZANIA

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MUNISHI, P. K. T., SHEAR, T. H., WENTWORTH, T. & TEMU, R. A. P. C. 2007. Compositional gradients of plant communities in submontane rainforests of eastern Tanzania. This study classified plant communities and examined the environmental correlates of community compositions in two submontane rainforests on the ranges of Eastern Arc Mountains, Tanzania. Using agglomerative cluster analysis, indicator species analysis and non-metric multidimensional scaling (NMS) ordination, based on importance value of tree species, five distinct plant communities were identified in the Usambara and six in the Uluguru mountains. The communities corresponded closely to variations in topography and soil physical and chemical properties. The different communities occurred on clay soils in lower elevations and on sandy-clay to sandy-clay-loam soils in higher elevations. Two topographic and 14 edaphic factors were significant correlates of plant community composition. Elevation was the strongest correlate of community composition on individual mountain range followed by percent clay and soil pH. Landform index and soil Na concentration were the major factors in separating plant communities on the west Usambara and Uluguru Mountains. There were appreciable variations in plant community compositions and patterns on the two mountain ranges. The results suggest that plant community patterns in the Eastern Arc Mountains vary from one range to another and are influenced by a complex of local heterogeneity in topographic and edaphic factors. The complex of factors influencing plant distribution can have a big bearing in species restoration and biodiversity conservation in the Eastern Arc Mountains.

Keywords: Cluster analysis, Eastern Arc Mountains, biodiversity, non-metric, multidimensional scaling, ordination, species association, West Usambara, North Uluguru

MUNISHI, P. K. T., SHEAR, T. H., WENTWORTH, T. & TEMU, R. A. P. C. 2007. Kecerunan komposisi bagi komuniti tumbuhan di hutan hujan subgunung di Tanzania timur. Kajian ini mengelaskan komuniti tumbuhan dan mengkaji faktor korelasi alam sekitar bagi komposisi komuniti dua hutan hujan subgunung di banjaran Pergunungan Arka Timur, Tanzania. Dengan menggunakan analisis kelompok aglomerat, analisis spesies penunjuk dan penskalaan berbilang matra (NMS), dan berasaskan indeks nilai kepentingan spesies pokok, lima komuniti yang jelas dikenal pasti di pergunungan Usambara and enam di pergunungan Uluguru. Komuniti tersebut sepadan dengan variasi topografi serta sifat fizikal dan kimia tanih. Pada aras ketinggian yang lebih rendah, komuniti yang berbeza itu wujud di atas tanah liat manakala di aras yang lebih tinggi, komuniti tersebut terdapat di tanih campuran pasir, tanah liat dan loam. Dua faktor topografi dan 14 faktor edafik merupakan faktor korelasi yang signifikan bagi komposisi komuniti tumbuhan. Ketinggian merupakan faktor korelasi yang terkuat bagi komposisi komuniti di banjaran pergunungan. Ini diikuti oleh peratus tanah liat dan pH tanih. Indeks bentuk tanah dan kepekatan Na tanih ialah faktor utama yang memisahkan komuniti tumbuhan di Pergunungan Usambara barat dan Pergunungan Uluguru. Terdapat variasi yang agak besar dalam komposisi serta corak komuniti tumbuhan di kedua-dua banjaran pergunungan. Keputusan kami mencadangkan bahawa corak komuniti tumbuhan di Pergunungan Arka Timur berbeza daripada satu banjaran kepada yang lain dan dipengaruhi oleh pelbagai keheterogenan tempatan dalam faktor topografi serta edafik. Faktor-faktor ini yang mempengaruhi taburan tumbuhan memberi kesan besar dalam pemulihan spesies serta pemuliharaan biodiversiti di Pergunungan Arka Timur.

INTRODUCTION

Composition gradients are the complex of factors of the environment to which plant species respond to differently to form distinct associations with different composition. Plants

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will usually grow in areas where there are favourable conditions for them to survive and reproduce. Where conditions are not favourable only a few plants that are adapted to this kind of environment will survive. There are various factors that influence the growth of plants in a particular environment. These include moisture, soil physical and chemical properties and other physical characteristics of the landscape. Plant distribution may show very big variations within a landscape as influenced by different environmental factors (Lovett *et al.* 2001, Munishi 2001). Plants that respond to the same environmental factors equally will usually associate to form distinct plant communities.

Since plants only grow in areas where the soil is favourable then the variations of soil across the landscape will influence the distribution and association of the vegetation. Soil properties vary across landscape and vegetation patterns and species associations within a given landscape are influenced by limitations and opportunities advanced by variations in the operating environmental factors in that landscape (Munishi 2001). Such environmental factors may promote or limit growth and propagation depending on species adaptation to those factors.

The rainforests of Tanzania occupy small areas mostly confined to isolated mountains. Most of these forests are under intense deforestation pressure with the remaining forests gazetted as reserves managed as catchment forests for rainwater capture and biodiversity conservation. In contrast, most lowlands are either dry or have been deforested for agriculture.

The Eastern Arc Mountain forests are recognized for their unique and diverse biota, with floristically rich forest vegetation that ranges from lowland rainforests to elfin montane forests. The Mountains are one of the world's 34 biodiversity hotspots (Conservation International 2006). The level of endemism of the 2100 known species of vascular plants has been estimated at 25–39%. Some six families have high endemism ranging from 31% for Orchidaceae to 73% for Gesneriaceae, and more than 10 genera are considered endemic or near-endemic (Lovett 1988, 1989, Mittermeier *et al.* 1999).

Classification and assessment of vegetation patterns and species associations are important tools for land management, restoration and conservation. With time deforested mountain areas in the Eastern Arc will lose their agricultural productivity and are likely to be abandoned because of insufficient crop yield. The knowledge of plant community dynamics and species associations as influenced by varying environmental factors is important in restoration of forest biodiversity in degraded parts of the mountains as well as *in situ* biodiversity conservation.

Past assessments of variations in plant communities in the Eastern Arc Mountains of Tanzania have mainly been based on variations in elevation and climate (Hall 1980, Lovett 1990, 1996, Pócs *et al.* 1990). However, temperature, soil and precipitation also influence vegetation distribution in the Eastern Arc Mountains of Tanzania (Lovett 1990). Further, majority of the studies in the northern part of the Eastern Arc were concentrated more on the East Usambara mountains while the Uluguru mountains have not been covered much due to access restrictions that existed. Research on the Ulugurus has just started recently among the Eastern Arc ranges. Since mountain rainforest environments are very variable for plant growth, species distribution, diversity and plant community patterns may be associated with location specific complex of interacting environmental factors. This study classified plant communities and assessed the environmental correlates of plant community composition in the West Usambara and Uluguru submontane rainforests of the Eastern Arc Mountains of Tanzania.

MATERIALS AND METHODS

Study sites

The Eastern Arc Mountains are a chain of crystalline mountains near the Indian Ocean coast stretching from southern Tanzania to southern Kenya (8° 51' S, 34° 49' E to 3° 2' S, 38° 20' E). This chain is several mountain ranges (Figure 1) separated by lowlands that originated from block faulting, dating back to the Karoo period approximately 300 million years ago (Lovett 1996). These mountains support some of the most luxuriant montane and submontane rainforests of eastern and central Africa. The most important Eastern Arc Mountains in Tanzania with rainforests include South Pare, West Usambara, East Usambara, Nguu, Nguru, Ukaguru, Uluguru, Rubeho, Malundwe, Uzungwa and Mahenge. The foci of

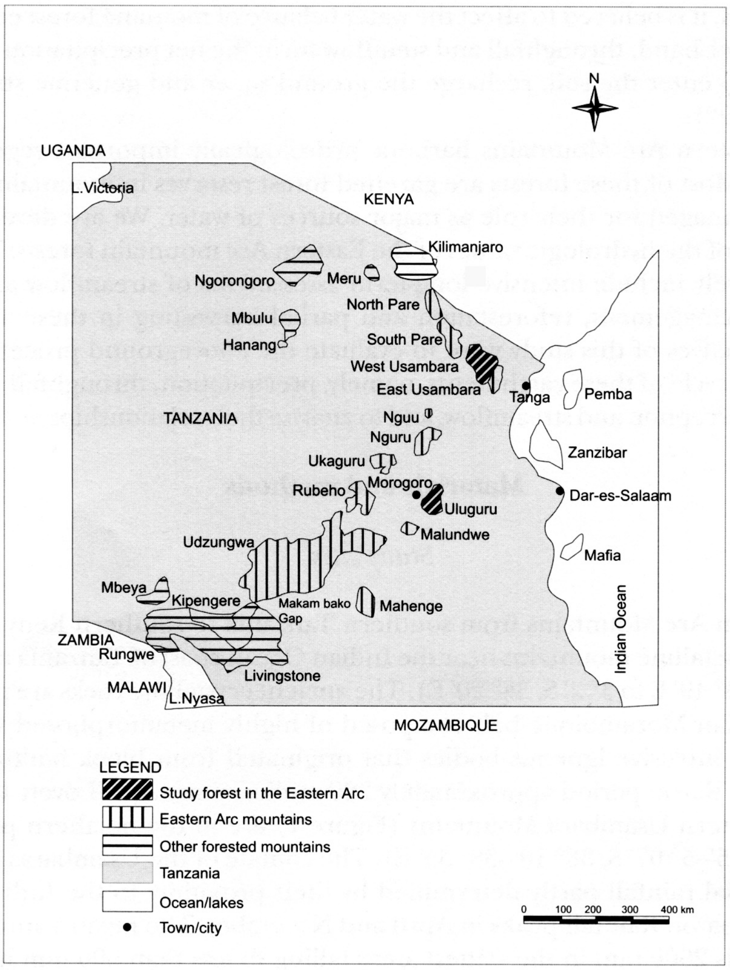

Figure 1 A map of Tanzania showing the Eastern Arc Mountains and the forests in which the study was conducted

this study were the Mazumbai and Kisimagonja Forest Reserves in the West Usambaras and the Uluguru north Forest Reserve in the Ulugurus.

The West Usambara range is in the northern part of the Eastern Arc Mountains (4° 25' S–5° 07' S and 38° 10'–38° 35' E). The geology is composed of late Pre-Cambrian metamorphic rocks of gneiss type of the Usagara System, with two main highland soil types, namely, the humid ferrisols in the drier areas and humic ferralitic soils in the more humid and wet areas (Hall 1980, Tosi *et al.* 1982). The climate is oceanic with bimodal rainfall partly determined by proximity to the Indian Ocean and the equator. Rainfall peaks in April and November with a mean annual rainfall maximum of 2000 mm in the wettest areas, falling to less than 600 mm in the drier areas. Moist forests cover extensive areas of the wetter eastern and southern sides of the mountains. The Mazumbai (840 ha) and Kissimagonja (2840 ha) Forest Reserves have among the highest rainfall in the West Usambaras. Monthly rainfall averages > 50 mm and mean annual rainfall is 1300 mm. The elevation ranges from 1300 to 1910 m. The vegetation consists of lower montane, submontane and montane evergreen rainforests.

The Uluguru range (7° 2'–7° 16' S and 38° 0'–38° 12' E) is in the central part of the Eastern Arc Mountains. The Uluguru bedrock is made up of Pre-Cambrian metamorphic rocks dominated by hornblende-pyroxine granulites with injections of granite and gneiss. The climate is oceanic with bimodal rainfall, also peaking in April and November. The annual rainfall is 2900–4000 mm on the eastern windward slopes and 1200–3100 mm on the western leeward slopes. The eastern windward slopes experiences over 100 mm of rainfall every month. The elevation ranges from 1600 to 2300 m and the vegetation consists of submontane and montane rainforests. The north Uluguru (8357 ha) Forest Reserve covers an altitude range between 1600 and 2220 m. These mountains were chosen to represent the northern extent and the central parts of the Eastern Arc Mountains of Tanzania.

Data collection

A total of 100 plots of size 0.02 ha (20 × 10 m) were established in each of the two ranges. The plots were established along parallel lines with starting points subjectively chosen to cover as much variation as possible from valley bottoms to ridge tops. Plots were laid with their long axis perpendicular to the slope to minimize within-plot variations and maximize between-plot variations. The following information were collected at each plot: diameter at breast height (dbh, 1.3 m) of all trees ≥ 6 cm (for buttressed trees, diameters were measured above the buttress), occurrence of all other plant species (trees < 6 cm dbh, shrubs, and herbs) assessed within a 2-m strip along the centre line of the plot, elevation, slope, aspect, landform index (LFI) and terrain shape index (TSI) (McNab 1989, 1993). Species botanical names were identified and confirmed at the National Herbarium of Tanzania.

Soil samples were collected at 0–15 cm and 15–30 cm depths at three equidistant points along the plot center line. The soil samples from each point in a plot were mixed to form one sample for each depth.

The samples were ground and passed through a 2-mm sieve. Concentrations of Ca, Mg, K, Na, Cu, Al and Zn were analyzed by inductively coupled plasma-atomic emission spectrometry using a Varian Liberty Series 2 ICP analyzer. Ammonia was determined spectrophotometrically with a Lachat QuickChem 8000 System Autoanalyzer (Ranger and Diamond, Lachat Instruments), method 31-107-06-1. Cation exchange capacity (CEC) was determined using the method of Zelazny *et al.* (1996). The effective cation exchange capacity (ECEC) was the sum of Ca, Mg, K, Na and Al concentrations. Total basic cation concentration (CAT) was the sum of Ca, Mg, K and Na concentrations. Percent cation saturation was the ratio of cation concentration to the ECEC. Percent base saturation (%BS) was determined as the ratio of total basic cation concentration to CEC. Percent carbon and nitrogen were determined using a CHN elemental analyzer, model NC2100, CE Instruments. Soil texture was determined by the hydrometre method (Sheldrick & Wang 1993). Soil pH was measured electrometrically using 10 g of soil sample diluted by deionized water in a ratio of 1:2. Due to their close proximity, data from Mazumbai and Kisimagonja Reserves were combined to form one West Usambara Forest description.

Data analyses

The importance value (IV) of each species in each plot was computed as the average of relative basal area and relative density. Aspect was transformed as in Beers *et al.* (1966):

$$A' = \cos(A_{max} - A) + 1$$

where
A' = transformed aspect
A = the direction of the prevailing slope measured in azimuth degrees clockwise from the north
A_{max} = the azimuth to be assigned the highest numerical value on the transform scale = 45

The plots from the two ranges were separately classified by agglomerative hierarchical cluster analyses of the species IV index (Orloci 1967) using Sørensen's distance measure and a group linkage method with flexible β of -0.55. The plots were ordinated by non-metric multidimensional scaling (NMS) using the PC-ORD version 4.0. The topographic and edaphic variables were correlated with plant community composition in the NMS ordination. Indicator species analysis was performed using the method of Dufrene and Legendre (1997) contained in the PC-ORD version 4.0.

For the analysis of similarities between forest types on the two ranges, the plots from the Usambara and Uluguru were combined in one ordination consisting of all 200 plots (100 from each of the forests) irrespective of differences in elevation. To compare forests at similar elevations in the Uluguru and Usambara ranges, all plots with overlapping elevations (42 in the Usambara and 68 in the Uluguru) were combined and ordinated separately in an attempt to filter out effects caused by differences in elevations (Lovett 1996).

Community types in each range were determined from agglomerative classifications, ordinations and indicator species analysis. Community types were named following procedures of the Nature Conservancy (Anderson *et al.* 1998) where names of dominant and diagnostic species are used as the foundation of the association name. Communities were named by the first three to four member species with the highest percent IV, constancy and significant indicator values (p = 0.05) (Dufrene and Legendre 1997). Member species for a given association (community) would not have a higher constancy in another community than that in its faithful association(s) (Barbour *et al.* 1987).

RESULTS

Compositional gradients, plant community classification and description in the Usambaras

From the ordination diagram (Figure 2) and significance of the indicator species (Table 1) five distinct plant communities were characterized in the west Usambara. One topographic and six edaphic factors were associated with plant communities and species distribution (Figure 2). Elevation (which may be a surrogate of climatic factors) was the strongest correlate of community composition, followed by percent clay, percent nitrogen (%N_{30}) percent carbon (%C_{15}), sodium concentration $[Na]_{30}$, percent sand and percent potassium saturation (%$[K]SAT_{15}$) (parameters followed by a subscript 15 represent data from the 0–15cm depth, those followed by a 30 are from the 15–30 cm depth). Potassium was a strong gradient as a percent cation saturation of ECEC but not as an individual cation. Plant communities were ordered along the second axis of the ordination, which was positively correlated with elevation, %N_{30}, %C_{15}, %sand and $[Na]_{30}$ and negatively correlated with %clay. Axis 1 of the ordination was negatively correlated with %$[K]SAT_{15}$ (Figure 2). *Syzygium guineense-Sorindeia usambarensis-Parinari excelsa-Newtonia buchananii* forest responded more to %$[K]SAT_{15}$. Three communities occurred on clay soils at low elevations and two on sandy-clay-loam soils at higher elevations.

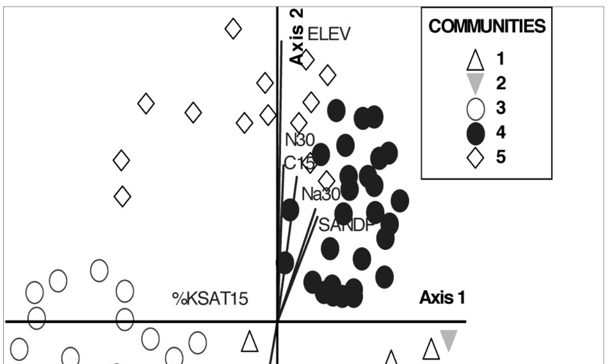

Figure 2 Compositional gradients and plant communities in NMS ordination of 100 vegetation plots in the west Usambara submontane rainforests, Eastern Arc Mountains of Tanzania. Five communities were recognized as influenced by different topographic and edaphic factors. ELEV = elevation (m), %$KSAT_{15}$, = percent K saturation at 15 cm depth, CLAYP = % clay, SANDP = % sand, C_{15}, N_{30} = % nitrogen and carbon, Na_{30} = concentrations of Na at 30 cm depth. The communities: 1 = *Sorindeia usambarensis-Parinari excelsa-Newtonia buchananii* forest, 2 = *Strombosia scheffleri-Craibea brevicaudata-Pachystela msolo-Isoberlinia scheffleri* forests, 3 = *Syzygium guineense-Sorindeia usambarensis-Parinari excelsa-Newtonia buchananii* forest, 4 = *Ocotea usambarensis-Syzygium guineense-Parinari excelsa* forest, 5 = *Agauria salicifolia-Ocotea usambarensis-Cryptocaria liebertina* forest.

Table 1 Plant communities and species associations in a submontane rainforest in the Usambara, Eastern Arc Mountains of Tanzania

Community	Most abundant species	IV* (%)	Constancy (%)	Elevation (m)		S**	Soil type
				Range	Mean		
Sorindeia usambarensis	*Sorindeia usambarensis*	23 (41)	93				Clay
-Parinari excelsa-	*Parinari exelsa*	17 (37)	79		1468[1]		
Newtonia buchanani	*Newtonia buchanani*	14 (27)	57	1360–	50[2]		
forest	*Allanblackia stuhlmanii*	8 (35)	57	1650	50[3]	32	
Strombosia scheffleri-	*Strombosia scheffleri*	9 (58)	88				clay
Craibea brevicaudata-	*Craibia brevicaudata*	9 (46)	48				
Pachystela msolo-	*Pachystela msolo*	9 (31)	36				
Isoberlinia scheffleri	*Isoberlinia schefleri*	9 (30)	40				
forest	*Drypetes usambarica*	8 (38)	52		1515[1]		
	Dicranolepis usambarica	8 (23)	36	1390–	72[2]		
	Cola greenwayii	5 (28)	48	1840	28[3]	39	
Syzygium guineense-	*Syzygium guineense*	37 (77)	100				clay
Sorindeia usambarensis-	*Sorindeia usambarensis*	19 (38)	100		1527[1]		
Parinari excelsa-	*Parinari excelsa*	9 (18)	68	1415–	74[2]		
Newtonia buchanani forest	*Newtonia buchanani*	9 (15)	53	1800	26[3]	33	
Ocotea usambarensis-	*Ocotea usambarensis*	41 (78)	100		1662[1]		sandy-
Syzygium guineense-	*Syzygium guineense*	7 (10)	71	1430–	54[2]		clay-
Parinari excelsa forest	*Parinari excelsa*	7 (37)	68	1880	46[3]	48	loam
Agauria salicifolia-	*Agauria salicifolia*	20 (77)	79				sandy-
Ocotea usambarensis-	*Ocotea usambarensis*	11 (15)	71		1770[1]		clay-
Cryptocaria liebertina forest	*Cryptocaria liebertina*	7 (42)	50	1570–	43[2]		loam
	Aphloia theiformis	5 (37)	79	1910	57[3]	49	

Numbers in parentheses show the species indicator values.
*IV = importance value
**S = Species richness
[1] = mean elevation for plots representing a given community
[2] = % of plots below the mean elevation for a given community
[3] = % of plots above the mean elevation for a given community

Compositional gradients, plant community classification and description in the Ulugurus

In the Ulugurus six distinct plant communities were identified (Figure 3). One topographic factor and six edaphic factors were significant correlates of community composition, with elevation being the strongest gradient. Other correlates of community composition in increasing order were pH_{30}, total cations (CAT_{15}) calcium concentration $[Ca]_{15}$, percent calcium saturation ($\%[Ca]SAT_{15}$), percent aluminum saturation ($\%[Al]SAT_{15}$) and magnesium concentration $[Mg]_{15}$. Calcium as an individual cation was as strong a gradient as percent calcium saturation of ECEC. Aluminum was a strong gradient as percent cation saturation of ECEC but not as an individual cation. Plant communities in the Ulugurus were ordered along the first axis, which was negatively correlated with elevation and $\%[Al]SAT_{15}$ and positively correlated with pH_{30}, CAT_{15}, $[Ca]_{15}$, $[Mg]_{15}$ and $\%[Ca]SAT_{15}$ (Figure 4). One community occurred on clay soil at lower elevations, one on sandy-clay soils at mid elevations, and four on sandy-clay/sandy-clay-loam soils at higher elevations (Table 2).

Combined analysis of the Usambara and Uluguru forests

When all the Usambara and Uluguru plots were combined into one classification and ordination, the two ranges separated out as two different communities ordered along axis 1 of the ordination though some plots from both ranges overlapped (Figure 4). Axis 1 of this ordination was negatively correlated with elevation, and positively correlated with $[Na]_{30}$ and CEC_{30} (Figure 4). Analysis of the Usambara and Uluguru plots with similar elevations (overlap) separated the two ranges into two completely

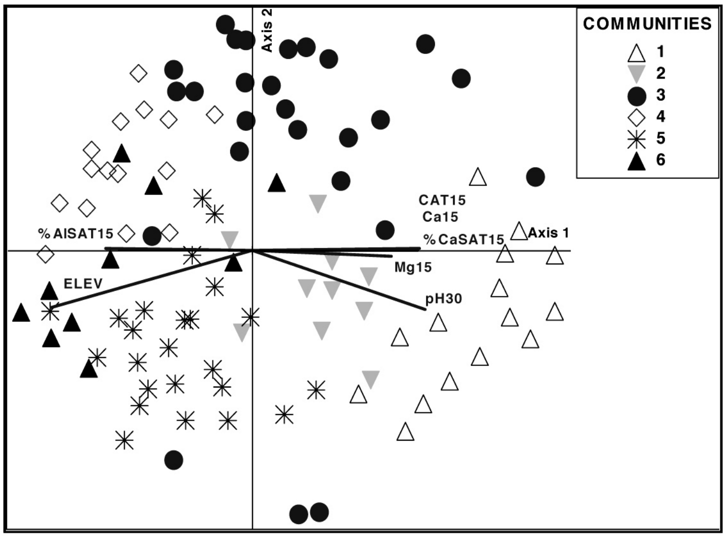

Figure 3 Compositional gradients and plant communities in NMS ordination of 100 vegetation plots in the Uluguru submontane rainforest, Eastern Arc Mountains of Tanzania. Six communities were characterized as influenced by different topographic and edaphic factors. ELEV = elevation (m), $\%AlSAT_{15,}$ $\%CaSAT_{15}$ = percent Al and Ca saturation at 15 cm depth, Ca_{15}, Mg_{15} = concentrations of Ca, and Mg, at 15 cm, pH_{30} = soil pH at 30 cm depth. The communities: 1 = *Myrianthus arborea-Cussonia spicata-Afrocrania volkensii-Albizia gummifera* forest, 2 = *Ocotea usambarensis-Rawsonia reticulate-Deinbolia kilimandscharica* forest, 3 = *Trichocypha ulugurensis-Strombosia scheffleri-Dasylepis integra* forest, 4 = *Symphonia globulifera-Cassipourea malosana-Syzygium guineense* forest, 5 = *Allanblackia ulugurensis-Cyathea usambarensis-Garcinia volkensii* forest, 6 = *Syzygium guineense-Lasianthus cereiflorus* forest.

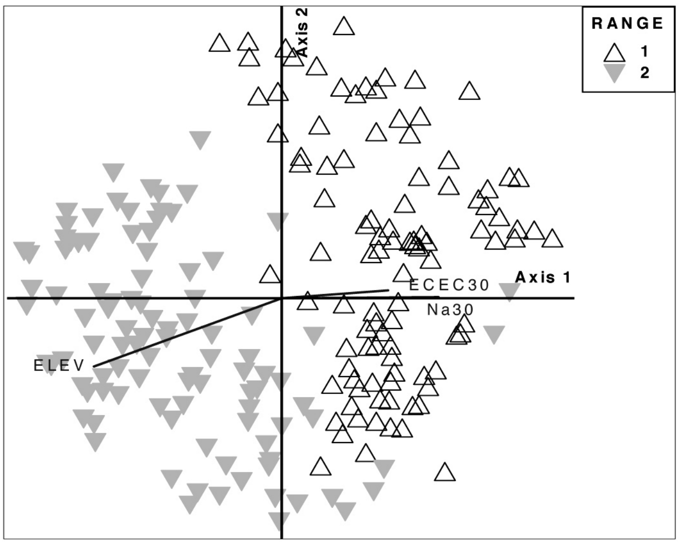

Figure 4 Compositional gradients and vegetation difference between two afromontane rainforests in NMS ordination of vegetation plots, Eastern Arc Mountains. The analysis covered all elevation ranges. Range 1 = West Usambara, Range 2 = Uluguru, ELEV = elevation, $ECEC_{30}$ = cation exchange capacity at 30 cm depth, Na_{30} = soil [Na] (c-mole kg^{-1}) at 30 cm depth, LFI = landform index. N_{30}, C_{15} = % nitrogen and carbon at 30 cm and 15 cm depth. There were some plot overlaps in the two ranges that may entail some similarities between the two ranges.

Table 2 Plant communities and species association in a submontane rainforest in the Uluguru, Eastern Arc Mountains of Tanzania

Community	Most abundant species	IV* (%)	Constancy (%)	Elevation (m)		S**	Soil type
				Range	Mean		
Myrianthus arborea-	*Myrianthus arborea*	13 (38)	57				
Cussonia spicata-	*Cussonia spicata*	12 (74)	50		1682[1]		clay
Afrocrania volkensii-	*Afrocrania volkensii*	11 (52)	43		57[2]		
Albizia gummifera - forest	*Albizia gummifera*	11 (34)	43		43[3]		
	Vitex doniana	6 (65)	29				
	Oncoba spinosa	5 (20)	43	1610–			
	Allophylus abysinicus	5 (54)	41	1820		41	
Ocotea usambarensis-	*Ocotea usambarensis*	25 (64)	88				sandy
Rawsonia reticulate-	*Rawsonia reticulata*	6 (17)	63				-clay/
Deinbolia kilimandscharica	*Deinbolia kilimandscharica*	5 (14)	55		1903[1]		sandy
forest	*Strychnos scheffleri*	5 (10)	54	1700–	57[2]		- clay -
	Memecylon veruculosum	5 (10)	54	2140	42[3]	57	loam
Trichocypha ulugurensis-	*Trichocypha ulugurensis*	12 (35)	74				sandy
Strombosia scheffleri-	*Strombosia scheffleri*	11 (36)	61				-clay
Dasylepis integra forest	*Dasylepis integra*	11 (23)	74		1750[1]		
	Ficalhoa laurifolia	9 (19)	26	1610–	48[2]		
	Newtonia buchananii	6 (17)	26	1900	52[3]	50	
Symphonia globulifera-	*Symphonia globulifera*	23 (56)	100				sandy
Cassipourea malosana-	*Cassipourea malosana*	9 (36)	67				-clay
Syzygium guineense forest	*Syzygium guineense*	9 (13)	67				
	Chrysophyllum gorungosanum	8 (45)	60				
	Zenkerella capparidacea	7 (66)	80				
	Parinari exelsa	6 (11)	17		1901[1]		
	Dasylepis integra	6 (27)	16	1790–	63[2]		
	Tabernaemontana ventricosa	5 (18)	16	2010	37[3]	37	
Allanblackia ulugurensis-	*Allanblackia ulugurensis*	9 (40)	71				sandy
Cyathea usambarensis-	*Cyathea usambarensis*	9 (55)	58				-clay-
Garcinia volkensii forest	*Garcinia volkensii*	5 (30)	38		2059[1]		loam
	Olea europaea ssp. *africana*	5 (17)	42	1690–	46[2]		
	Prunus africana	5 (16)	41	2280	54[3]	59	
Syzygium guineense-	Syzygium guineense	26 (64)	78				sandy
Lasianthus ceruflorua	*Lasianthus cereiflorus*	24 (34)	71		1922[1]		-clay-
forest	Maytenus sp.	19 (33)	55	1190–	50[2]		loam
	Podocarpus milanjianus	17 (19)	56	2260	50[3]	36	

Numbers in parentheses show the species indicator values.
*IV = importance value
**S = Species richness
[1] = mean elevation for plots representing a given community
[2] = % of plots below the mean elevation for a given community
[3] = % of plots above the mean elevation for a given community

distinct communities ordered along axis 1 of the ordination, without any overlap (Figure 5). Axis 1 of this ordination was negatively correlated with landform index and positively correlated with CEC_{30}, $\%N_{30}$, $\%C_{15}$ and $[Na]_{30}$ (Figure 5). Axis 2 seems to separate communities responding to a complex of $[K]_{15}$, $[Al]_{15}$, $[Mg]_{30}$ and %BS (Figure 5).

DISCUSSION

The different communities identified in this study (Tables 1 and 2) are more refined forest types of the afromontane and transitional rainforests of White's (1983) classification of the vegetation of Africa, and other classifications of the Eastern Arc vegetation which were essentially based on elevation, and/or bioclimatic characteristics of the region (Lovett 1990, Poc's *et al.* 1990, Tosi *et al.* 1982). Characteristic species of the afromontane and transitional rainforests of these classifications were similar to those identified in the present study, with vegetation grouped into one or two general forest types. The present classification was based on species dominance, constancy and indicator values as influenced

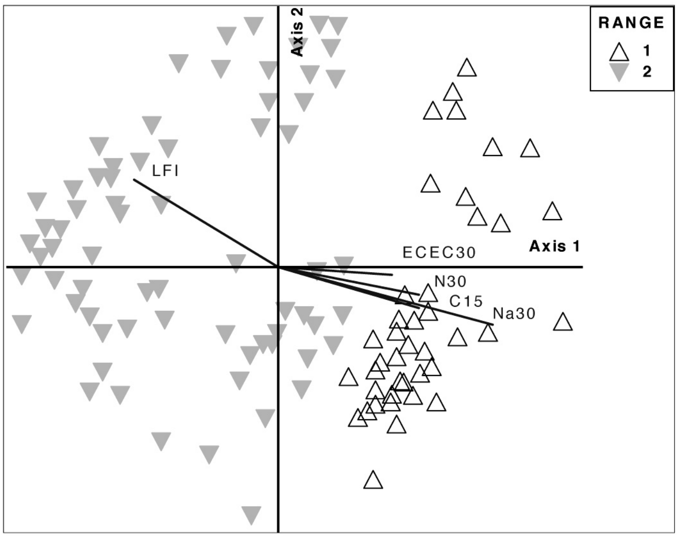

Figure 5 Compositional gradients and vegetation difference between two submontane rainforests in NMS ordination of vegetation plots in the west Usambara and Uluguru Eastern Arc Mountains. The analysis considered overlapping elevations. Range 1 = West Usambara mountains, Range 2 = Uluguru mountains, ELEV = elevation, $ECEC_{30}$ = cation exchange capacity at 30cm depth, Na_{30} = soil [Na] (c-mole kg^{-1}) at 30 cm depth, LFI = landform Index, N_{30}, C_{15} = % nitrogen and carbon at 30 cm and 15 cm depth. The two ranges separate into two forest vegetation types indicating dissimilarities in vegetation at similar elevations between the two ranges.

by soil physical and chemical properties. The *Ocotea usambarensis-Syzygium guineense-Parinari exelsa* forest and the *Agauria salicifolia-Ocotea usambarensis-Cryptocarya liebertina* forest in the present study may fit into the tropical montane moist forests defined by Tosi *et al.* (1982). Similarly, in the Uluguru range, with mean annual rainfall over 2000 mm and altitude of more than 1600 m, the plant communities are in the tropical pre-montane to lower montane wet forests life zone (Holdridge *et al.* 1971).

Plant communities grew at lower elevations and on different soil types in the Usambaras than in the Ulugurus (Tables 1 and 2). Though plant communities differed on the two ranges, several species including *S. guineense, O. usambarensis* and *S. schefleri* were common to both ranges. Several species occurred either in the Usambaras or in the Ulugurus but not in both (Tables 1 and 2). Some species such as *S. guineense*, *P. exelsa*, *S. usambarensis* and *O. usambarensis* seemed to have wide distributions in the different ranges and were dominant in more than one community. *Parinari exelsa* seemed to have a wider ecological range in the Usambaras as it occurred in more than two communities (Table 1).

Generally, elevation was the strongest correlate of community composition in both forests, followed by a number of edaphic factors that differed from one range to another (Figures 2 and 3). Some edaphic factors were strong gradients in the form of cation saturation of the effective cation exchange capacity (ECEC) but not as individual cations. Correlation analysis showed no significant correlation among the factors and, thus, they seemed to act independently in influencing species distribution in both forests. Percent cation saturation of the ECEC for some nutrients has proven a successful index in agronomic studies (J. Smyth 2001, pers. comm.). Although plants are most sensitive to nutrient concentrations in solution, generally, the proportions of cations in solution relative to total cations are correlated with the proportion of cations on the exchange complex and can be more robust indicators as to whether nutrient reserves or toxicity (Al) differ among plant communities. Other studies have also shown species composition to be more closely related to gradients in soil characteristics and topography (e.g. Lovett 1996, Webb & Peart 2000).

Although plant communities are distinct from one another, there is substantial species overlap in elevation ranges covered by different communities as well as species gradation from one community to another (Tables 1 and 2). A continuous variation in vegetation along an elevation gradient in afromontane forests has been discussed (Hamilton *et al.* 1989). However, Lovett (1996) could not find zones of vegetation in the forests of the Eastern Arc Mountains using presence-absence data. On the other hand Lovett *et al.* (2001) observed that the majority of restricted range forest tree taxa had restricted elevational ranges with 73.3% occurring in no more than 200 m elevational bands. Lieberman *et al.* (1996) found no discontinuities in vegetation distribution for a tropical forest in Costa Rica. However, Friis and Lowesson (1993) suggested altitudinal discontinuities in the vegetation of north-eastern Africa.

Using species IVs as a criteria for classification of plant communities, one may be tempted to label some communities as 'mixed' with no particular species dominance. This is the case with the putative communities *S. scheffleri-Craibea brevicaudata-Pachystela msolo-Isoberlinia schefleri* in the west Usambara and *Myrianthus arborea-Cussonia spicata-Afrocrania volkensii-Albizia gummifera*, *Trichocypha ulugurensis-Strombosia scheffleri-Dasylepis integra* and *Allanblackia ulugurensis-Cyathea usambarensis-Garcinia volkensii* in the Uluguru forests. On the other hand, if IVs, constancy and indicator values of both species are used concurrently these putative communities can show a strong species dominance to justify naming them by particular species. One community is characterized by *Vitex doniana* and *Oncoba spinosa,* which are woodland species. The Uluguru study extended into the lower slopes of the leeward (dry) part of the mountain which is bordered by woodland vegetation in the lower part. Thus, migration of such species probably in the transition zone between the woodland and lower montane vegetation could occur.

Considering that different species respond uniquely to different environmental factors and that each species will survive where conditions allow them to grow, the observed patterns of species association into communities can have a big bearing in management for conservation of forest biodiversity (Lovett *et al.* 2001). Plant community patterns of the west Usambara and the Uluguru Mountains are results of complex factors arising from local variations in physical environment, especially soil factors, and cannot be associated only to common evolution of the mountains, rainfall and oceanic influence. Also latitudinal differences cannot be attributed to observed patterns of tree species associations (Lovett 1996, Lovett *et al.* 2001). The landform index, which was observed to separate plant communities between the Uluguru and Usambara ranges, has been shown to be a strong measure of soil depth, moisture and nutrient redistribution and is an important modifier of the mesoscale environment for plant growth (Edward 1994).

CONCLUSIONS

The west Usambara and Uluguru Mountains have different patterns of plant communities and plant species associations determined by complex topographic and edaphic factors. Within a single range, elevation and soil factors (particularly texture, CEC, CAT, [Al], soil pH, percent clay, percent carbon and percent nitrogen) play key roles in plant distribution. Landform index plays the most important role in inter-range differences. There are elevation-induced changes in species composition but variations in edaphic factors play key roles in shaping plant community patterns. This complex of factors is an important consideration in designing restoration and biodiversity conservation programmes.

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