RESEARCH PAPER

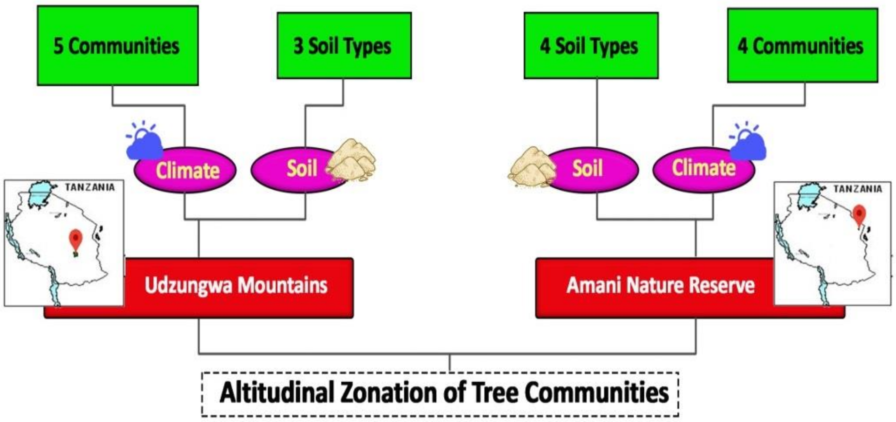
Altitudinal zonation of tree communities along climate and soil gradients in the East African biodiversity hotspot

Alfred Kahanju Chitiki *
Department of Ecosystems and Conservation, College of Forestry, Wildlife and Tourism, Sokoine University, Tanzania

Highlights

- Climate role in vegetation of wet Montana forests is important.
- Altitudinal zonation of tree communities along climate and soil gradients was studied.
- All studied communities correlated with acidic soils in ANR and UMF.
- Variable results might be due to different sampling approaches and environmental factors used.

Graphical Abstract



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Abstract

Using climate and soil parameters, zonation of tree communities and species associations were classified along altitudinal gradients of Amani Nature Reserve (ANR) and Udzungwa Mountains (UMF). The plots were sampled from the two mentioned sites and classified separately. In addition, tree communities were named based on dominant and diagnostic species. Along climate gradient, four and five distinct plant communities were identified in ANR and UMF respectively. The communities consisted of typical Miombo species in the lowland forests (lower slopes) of the UMF. Zonation of the tree communities corresponded to a range of edaphic factors. The communities of ANR responded to sand, loamy sand, and sandy clay soil types, while in UMF the communities correlated with sandy loam and loamy sand soil types. All communities correlated with acidic soils in ANR and UMF. This study advances the understanding of drivers of plant community distribution in EAMs and other tropical ecosystems. Variation findings reported in some of the previous studies might be due to different sampling approaches and variables (environmental factors) used in the analysis.

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* Corresponding author: a.k.chitiki@gmail.com (A.K. Chitiki)

1. Introduction

Variation in floristic patterns along elevational gradients has related to habitat heterogeneity, climate, biotic interactions, productivity, and history (Qian and Ricklefs, 2004). In EAMs, numerous researchers have attempted to understand the causes and patterns of forest zonation along elevational gradients (Lovett, 1996, Lovett, 1998; Lovett at al., 2006). However, the reasons for these patterns are complex and involve various interactions. For example, the decline in temperature with elevation has been related to lowering productivity and, consequently, a change in plant community pattern (Lieberman et al., 1996; Givnish, 1999). On the other hand, soils may interact with other abiotic factors (climate-driven responses) to find the species, which occupy a site based on their differential capacity, tolerance, and resource utilization. These differences seem to be applied as driving mechanisms in species coexistence in similar environments. The differences also describe broad-scale compositional differences among multiple resource gradients (Currie et al., 2004).

Elsewhere edaphic conditions, microclimate, and species interactions have been reported to structure vegetation composition at the local scale (Blundo et al., 2012). These factors often change rapidly along altitudinal gradients (Muenchow et al., 2013). Based on observations, climate role in wet montane forests' vegetation is important (Ashton, 2003; Beck et al., 2008). Moreover, water accessibility determines tropical dry forest communities (Punyasena et al., 2008). Similarly, soil conditions provide the necessities for the creature of tropical rain forests (Vazquez and Givnish, 1998). However, edaphic conditions in montane and tropical dry forests have shown less effect (Peña-Claros et al., 2012; Soethe et al., 2008). These environmental gradients and ecological interactions are essential in the structuring of plant communities. Therefore, in-depth analysis in floristic structuring with the particular environmental gradient is of great importance. Of the few studies linking floristic patterns to elevation in the EAMs (Lovett et al., 2006), none have used empirical climate data to infer such elevational gradients. Similarly, empirical studies linking edaphic factors to species plant community patterns in these sites are scarce. Analysis of edaphic correlates is important for improving understanding of the processes that drive floristic patterns and the coexistence of tropical tree species (Slik et al., 2003). Such studies may provide a useful understanding of climate and soil factors' influence in structuring vegetation communities in the EAMs. Therefore, this study aimed to describe the altitudinal zonation of tree communities along climate and soil gradients in ANR and UMF in the EAMs using imperical (extrapoted temperature) climate and soil data.

2. Materials and Methods

2.1. Study areas

The EAMs, located close to the Indian Ocean coast, is a chain of crystalline mountains from the Taita Hills in South-East Kenya to the Udzungwa Mountains in South-Central Tanzania (Lovett, 1999; Burgess et al., 2007). The studied area is stretcher between latitudes 3°2' S and 8°51' S and longitudes 34°49' E and 38°20' E. The EAMs range from sea level up to 2635 m in altitude. EAMs are a suitable hotspot habitat for hundreds of species found on earth. These species store one hundred million tons of carbon, which might otherwise release into the atmosphere and contribute to climate change (Burgess et al., 2007; Burgess et al., 2010; Clark, 2007). EAMs are also known worldwide for exceptional biodiversity value and high endemism in variable species (Brooks et al., 2002). The EAMs contain at least 800 endemic plant species (25% of the plant species), 10 endemic mammals, 19 endemic birds, 31 endemic reptiles, and 40 endemic amphibians. 78 vertebrate species, including 8 critically endangered species, were reported as threatened in the EAMs in the 2006 IUCN Red List. 20 out of 21 species of African violet grown in the EAMs are endemic (Burgess et al., 2007).

The first study area was Amani Nature Reserve (ANR), a portion of the East Usambara Mountain Forests shown in Fig. 1 (Tallents et al., 2005). It is located between latitudes 5° 14' S and 5°04' S and longitudes 38°30' and 38°40' E. The altitude of ANR is 1500 m, with an extensive plateau from 800–1000 m. The lower elevation forests are classified as lowland forests while at upper elevation as upper montane forests (Lovett, 1999). As one of the most biologically diverse forests in Africa, these mountains are of great importance due to at least 22% of plant species (Burgess et al., 2007; Kremen, 1994). The rainfall pattern is bimodal with a minor rainy season in November (Oct–Dec) and the main rain season in April (March-May) (Lovett, 1998).

The second study area was the Udzungwa Mountain block (Fig. 1). UMF is located 7°40′ S to 8°40′ S and 35°10′ E to 36°50′ E (Barelli et al., 2015). Field survey in this block was conducted at Udzungwa Mountains National Park (UMNP), Nyanganje Forest Reserve (NFR), and Udzungwa Scarp Forest Reserve in Kilombero and Kilolo Districts. The Udzungwa Mountains is the largest block of the EAMs, covering about 10 000 km^2 (Rodgers and Homewood, 1982). It is found on the southern end of EAMs chain. Udzungwa Mountain's highest point, Luhombero Peak, rises to 2800 m (Zilihona and Nummelin, 2001).

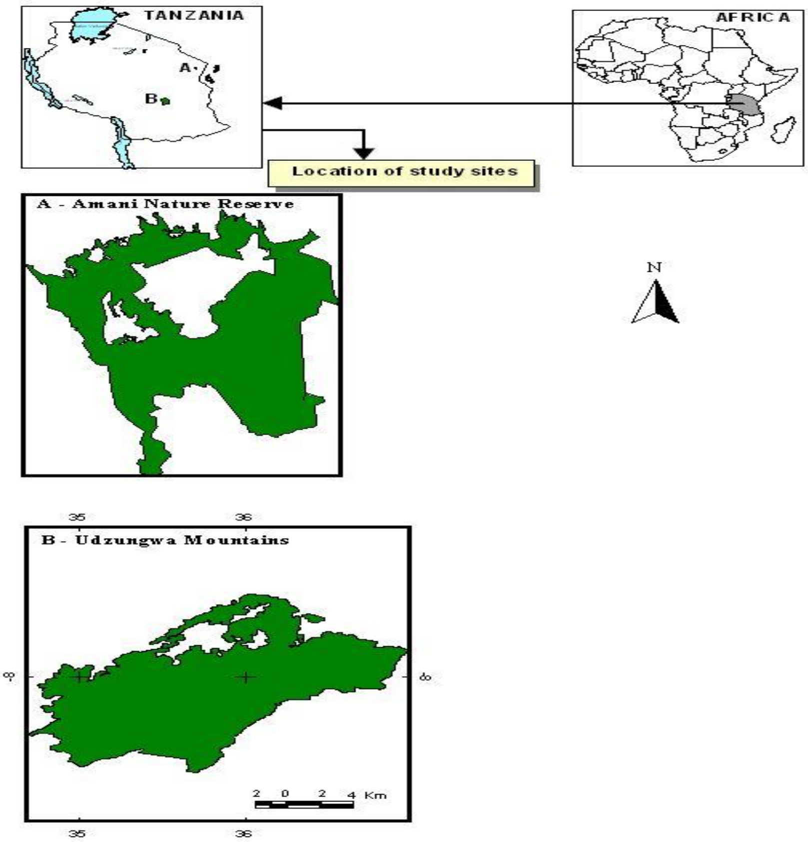

Fig. 1. The study area (Udzungwa Mountain block).

Depending on topography and distance from the Indian Ocean, rainfall varies. The eastern slopes situated face to the Indian Ocean have more than 2000 mm rainfall per year, whereas the western slopes are in the rain shadow, receiving about 600 mm precipitation per year. The rainfall pattern is unimodal, falling between November and May (Lovett, 1999). The eastern slope of the Udzungwa Mountains is of rare location left in the Afrotropical region, where a continuous moist forest is a cover from lowland (300 m) to highlands (2500 m). Soils are mostly sandy-loams or sandy-clay-loams (Lovett et al., 2006). The Udzungwa Mountains National Park, with an area of 1960 km^2, covers the wide portion of north-eastern Udzungwa Mountains. Nyanganje Forest Reserve is located between latitudes 7°56' S and 8°4' S and longitudes 36^{0}39' E and 36°50' E, 15 km northeast of Ifakara Township. The reserve covers the southeastern foothills of the Udzungwa Mountains (Tallents et al., 2005).

2.2. Plot establishment

Plots were established along altitudinal range from the lowland to montane forests of the ANR and UMF. The areas were stratified by elevation into lowland (<800 m), submontane (800 -1400 m), montane (1400-1800 m), and upper montane >1800 m (Lovett et al., 1997). In each strata, transects were systematically laid to cover as much variation as possible, and rectangular plots each 0.02 ha (20 m x 10 m) were laid along transects. The plots are big enough to keep environmental factors and forest structure homogeneous (Kluge et al., 2006). To minimize and maximize within-plot and between-plot variations, respectively, plots were laid with their long axes perpendicular to the slope in accordance. To ensure spatial heterogeneity in the dataset, the plots were located in different parts to cover as many landscape variations as possible (Barelli et al., 2015; Platts et al., 2013; Ter Steege et al., 2003).

2.3. Vegetation, climate, and soil data

In each plot, plant species were recorded both in their scientific (botanical) and local names. Voucher specimens of unidentified species were collected for further identification. Diameters at Breast Height (DBHs) for all trees were measured; large trees were measured using diameter tape while the veneer caliper was used for small trees. The DBH for buttressed trees were measured above the buttress. The information collected was used in subsequent assessment of species composition, richness, and diversity and associated plant communities (Kessler, 2001). Tree measurements were done following the standard vegetation monitoring protocol of the Tropical Ecology, Assessment, and Monitoring (TEAM) Initiative (Brown et al., 2005). A tree was judged to be in the plot if more than 50% of the trunk base was within the plot. Other parameters recorded include plot location and elevation using GPS for each plot .

Climate data for Amani Nature Reserve (ANR) and Udzungwa Mountains Forests (UMF) were obtained at weather stations with known elevations located near/within the study sites. For ANR, climate data were obtained from Marikitanda Tea Research Station while for UMF, data was obtained from Kilombero Sugar Company Limited, Ifakara Health Institute (Malaria Research), and Lower Kihansi Hydropower Project (Ferrer-Castan, D., Vetaas, 2005). In addition to vegetation and climate data, disturbances are assessed using disturbance transects. The levels of pole cutting, timber extraction, trapping, encroachment, and other human disturbances were assessed as a disturbance in a 10 m strip (5 m either side of the transect line) along the transect sub-divided into 50 m sections. Data for each 50 m section was separately recorded (Punyasena et al., 2008).

2.4. Data analysis

2.4.1. Climate data: temperature

Using data obtained from meteorological stations with known elevations located near/within the study sites, temperature extrapolations along elevational gradients were computed from linear regression of mean temperature versus elevation, assuming a decrease in temperature at a rate of 1 °C for every 100 m elevation band from reference points (Hawkins et al., 2008; Kessler, 2002). Hence temperature was assumed to decrease at a rate of 1 °C for every 100 m upslope and increase at the same rate downslope. Reference points in this study were the known elevations at which the meteorological stations are located. The regression equations presented in Table 1 were developed for maximum, minimum, and mean annual temperatures based on general linear function $y = mx + c$, i.e., Mean annual temperature (°C) = Slope x Elevation + Constant. The resulting equations were then used to estimate mean, minimum, and maximum temperature at each elevation of the sampled plots (Lomolino, 2001; Romdal and Grytnes, 2007).

2.4.2. Multivariate analysis

To investigate community changes with elevation, mean annual temperature, and disturbance, Canonical Correspondence Analysis (CCA) was used (Tattersfield et al., 2006). Canonical correspondence analysis was done on species abundance matrix (computed as basal areas for each species in the main matrix) (Palmer, 1993). A second matrix/environmental matrix consisted of the climate variables (elevation and mean annual temperature) in analyzing climate gradient and edaphic variables in analyzing soil gradient (Hart, 2006). The plots selected were separately classified by agglomerative hierarchical cluster analysis of the species basal areas. For this purpose, **S**ørensen's distance measure and a group linkage method with flexible β of -0.55 was used. Prior to analysis, the basal area for each species was computed for each plot. Community types in each site were determined from agglomerative classification and CCA ordination. Names of dominant and diagnostic species are used as the foundation of the association name. To name the Communities, the first 3 to 4 member species with the highest basal area are considered. CCA ordination and classification of community types were conducted via the PC ORD version 5.0.

Table 1. Regression models for estimating annual maximum, minimum, and mean temperatures (MAX, MIN, and MEAN) along an elevation gradient in ANR and UMF.

		Regression parameter	
Site	**Variable (° C)**	**Slope (m)**	**Intercept (c)**
ANR			
	Max	-0.01	34.4
	Min	-0.01	26.1
	Mean	-0.01	30.3
UMF			
Udzungwa Mountains National Park	Max	-0.01	34.4
	Min	-0.01	22.9
	Mean	-0.01	28.6
Nyanganje Forest Reserve	Max	-0.0099	43.0
	Min	-0.01	21.6
	Mean	-0.01	29.2
Udzungwa Scarp Forest Reserve	Max	-0.01	30.5
	Min	-0.01	27.7
	Mean	-0.01	29.1

3. Results and Discussion

3.1. Plant communities and species associations along a climate gradient

From agglomerative classifications and CCA ordinations, different plant communities were observed. Based on the dendrograms (Figs. 2 and 3) and species dominance estimated from basal areas, four and five determined plant communities were distinguished in ANR and UMF respectively and were characterized and presented according to species composition and associations (Tables 2 and 3). The plant communities for ANR were Isoberlinia scheffleri-Bombax rhodognaphalon-Parinari excelsa forest; Synsepalum msolo-Newtonia buchananii-Tricalysia dregeana forest; Bridelia micrantha-Vitex doniana-Ricinodendron heudelotii forest; and Ricinodendron heudelotii-Cephalosphaera usambarensis-Trichilia emetica forest while that of UMF were Brachystegia bussei-Burkea africana-Uapaca kirkiana forest; Parianari excelsa-Pteleopsis myrtifolia-Tricalysia pallens forest; Ricinodendron heudelotii-Newtonia buchanani-Antiaris toxicaria forest; Brachystegia boehmii-Parinari excelsa-Holarrhena pubescens forest; and Brachystegia spiciformis-Burkea africana-Uvariodendron pyconophyllums forest. These communities correlated to a range of environmental factors (Tables 2 and 3). Plant communities that correlated positively to elevation were negatively correlated to temperature (Figs. 3 and 5). Two communities occurred at low elevations/higher temperatures and two at mid (higher) elevations/lower ANR temperatures. Isoberlinia scheffleri-Bombax rhodognaphalon-Parinari excelsa and Bridelia micrantha-Vitex doniana-Ricinodendron heudelotii forests corresponded to lower elevations/higher temperature while Synsepalum msolo-Newtonia buchananii-Tricalysia dregeana and Ricinodendron heudelotii-Cephalosphaera usambarensis-Trichilia emetica forests corresponded to higher elevations/lower temperature (Table 2). Similarly, two communities occurred at low elevations, two at mid elevations and one community at higher elevations in UMF. Brachystegia bussei-Burkea africana-Uapaca kirkiana and Brachystegia spiciformis-Burkea africana-Uvariodendron pyconophyllums forests corresponded to lower elevations/higher temperature in UMF. These communities consist of typical Miombo species commonly found in the lowland forests (lower slopes) of the UMF. Parianari excelsa-Pteleopsis myrtifolia-Tricalysia pallens and Brachystegia boehmii-Parinari excelsa-Holarrhena pubescens forests corresponded to mid elevations whereas Ricinodendron heudelotii-Newtonia buchanani-Antiaris toxicaria forest corresponded to higher elevations/lower temperature (Table 3).

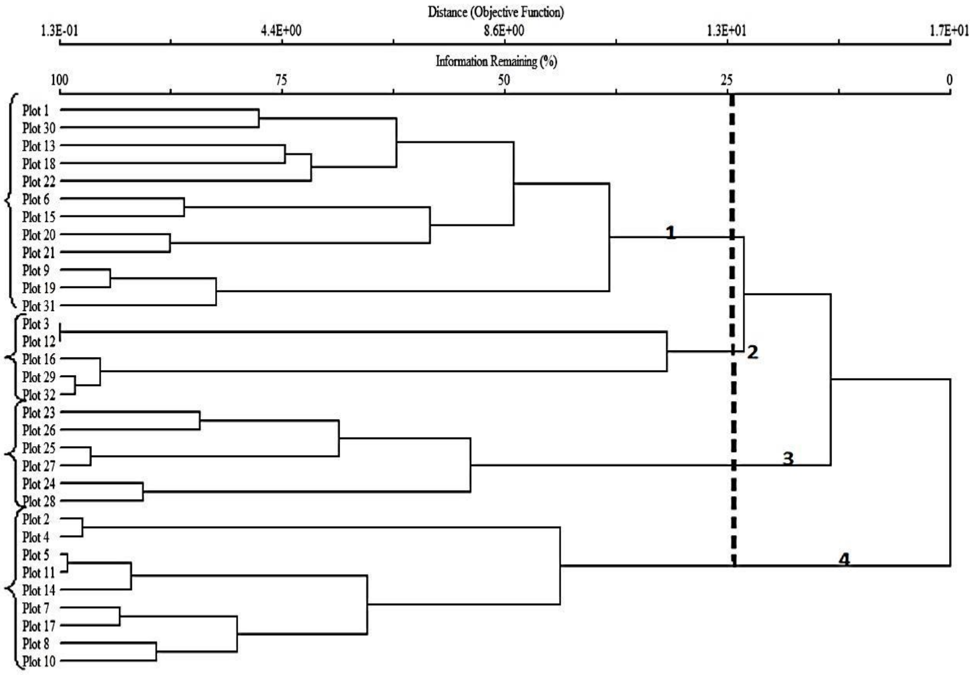

Fig. 2. Community dendrogram of Sørensen distances between plant communities along a climate gradient in Amani Nature Reserve, Eastern Arc Mountains of Tanzania. Communities are based on species dominance estimated from the basal area.

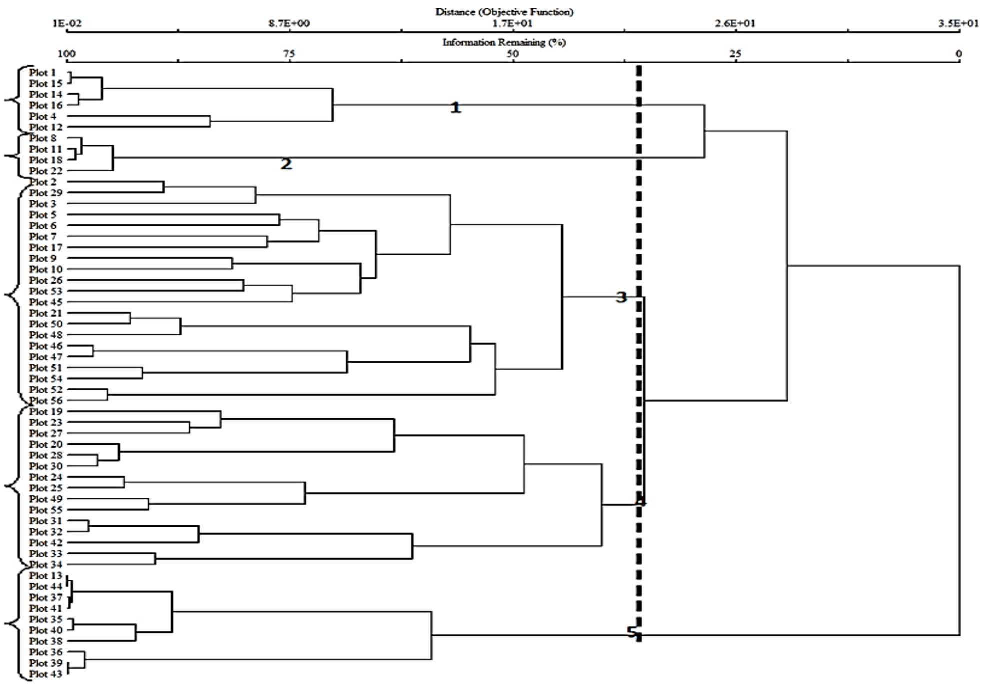

Fig. 3. Community dendrogram of Sørensen distances between plant communities along a climate gradient in the Udzungwa Mountains, Arc Mountains of Tanzania. Societies are base on species dominance estimated from the basal area.

Table 2. Plant communities and species associations along a climate gradient in Amani Nature Reserve, Eastern Arc Mountains of Tanzania.

Community	Associated species	Basal area (m²/ha)	Elevation (m)		Temperature (°C)	
			Range	Mean	Range	Mean
Isoberlinia scheffleri-Bombax rhodognaphalon-Parinari excelsa forest 1	Isoberlinia scheffleri	164.6				
	Bombax rhodognaphalon	88.3				
	Parinari excelsa	56.0	249-963	451	20.7-27.8	25.8
	Terminalia sambesiaca	45.8				
	Milicia excelsa	44.4				
	Chrysophyllum perpulchrum	36.2				
	Cedrella odorata	26.5				
	Sorindeia madagascariensis	22.7				
	Barringtonia racemosa	22.1				
Synsepalum msolo-Newtonia buchananii-Tricalysia dregeana forest 2	Synsepalum msolo	47.5				
	Newtonia buchananii	43.4	487-1088	793	19.4-25.4	22.4
	Tricalysia dregeana	30.7				
	Funtumia africana	28.2				
	Syzygium guineense	25.1				
	Greenwayodendron suaveolens	11.1				
	Drypetes gerrardii	10.6				
	Strombosia scheffleri	6.8				
	Isoberlinia scheffleri	6.6				
Bridelia micrantha-Vitex doniana-Ricinodendron heudelotii forest 3	Bridelia micrantha	15.6				
	Vitex doniana	12.4				
	Ricinodendron heudelotii	12.3	422-601	486	24.3-26.1	25.4
	Dombeya shupangae	9.7				
	Lonchocarpus capassa	8.7				
	Erythrina abyssinica	7.9				
Ricinodendron heudelotii-Cephalosphaera usambarensis-Trichilia emetica forest 4	Ricinodendron heudelotii	68.4				
	Cephalosphaera usambarensis	47.7				
	Trichilia emetica	37.7				
	Pterocarpus tinctorius	31.8	264-971	764	20.6-27.7	22.7
	Maesopsis eminii	25.6				
	Milicia excelsa	24.9				
	Annickia kummeriae	20.5				
	Funtumia africana	18.8				
	Quassia undulata	16.6				

Note: Numbers 1, 2, 3 and 4 represent the different plant associations on Fig. 2.

Table 3. Plant communities and species associations along a climate gradient in the Udzungwa Mountains, Eastern Arc Mountains of Tanzania.

Community	Associatedspecies	Basal area (m^2/ha)	Elevation (m)		Temperature (°C)	
			Range	Mean	Range	Mean
Brachystegia bussei-Burkea africana-Uapaca kirkiana forest 1	Brachystegia bussei	56.1				
	Burkea africana	11.9				
	Uapaca kirkiana	11.5				
	Diplorhynchus condylocarpon	7.1	326-531	412	23.9-25.7	24.9
	Pterocarpus tinctorius	6.3				
	Burkea africana	4.9				
	Brachystegia spiciformis	4.8				
	Dalbergia nitidula	2.6				
Parianari excelsa-Pteleopsis myrtifolia-Tricalysia pallens forest 2	Parianari excelsa	113.4				
	Pteleopsis myrtifolia	51.0				
	Tricalysia pallens	41.6	343-808	650	21.0-25.2	22.4
	Tabernaemontana usambarensis	11.1				
	Funtumia africana	1.4				
	Sorindeia madagascariensis	1.4				
	Tricalysia pivota	0.8				
Ricinodendron heudelotii-Newtonia buchanani-Antiaris toxicaria forest 3	Ricinodendron heudelotii	218.4				
	Newtonia buchanani	127.2				
	Antiaris toxicaria	109.5				
	Treculia africana	54.7				
	Bombax rhodognaphalon	50.8				
	Lettowianthus stellatus	35.9	340-1904	1195	10.1-25.2	17
	Ekebergia capensis	27.2				
	Anthocleista grandiflora	23.7				
	Allophyllus rubifolius	22.9				
	Macaranga capensis	22.6				
	Allanblackia stuhlmanii	21.3				
	Sorindeia madagascariensis	20.8				
	Premna senensis	18.1				
Brachystegia boehmii-Parinari excelsa-Holarrhena pubescens forest 4	Brachystegia boehmii	76.2				
	Parinari excelsa	24.7				
	Holarrhena pubescens	15.6				
	Tricalysia pallens	15.5	424-1798	875	11.1-25.0	20.4
	Pericopsis angolensis	15.2				
	Tabernaemontana usambarensis	12.9				
Brachystegia spiciformis-Burkea africana-Uvariodendron pyconophyllums forest 5	Brachystegia spiciformis	47.5				
	Burkea africana	8.5				
	Uvariodendron pyconophyllums	5.8				
	Pericopsis angolensis	5.4	324-601	437	23.2-26.0	24.8
	Brachystegia boehmii	5.1				

Note: Numbers 1, 2, 3, 4 and 5 represent the different plant associations on Fig. 3.

3.2. Plant communities and species associations along soil gradient

From agglomerative classifications and CCA ordinations, different plant communities were observed. Based on the dendrograms (Figs. 4 and 5) and species dominance estimated from basal areas, distinct plant communities were identified in ANR and UMF and were characterized and described based on species composition and associations. In ANR the plant communities were *Isoberlinia scheffleri-Bombax rhodognaphalon-Parinari excelsa* forest; *Synsepalum msolo-Newtonia buchananii-Tricalysia dregeana* forest; *Bridelia micrantha-Vitex doniana-Ricinodendron heudelotii* forest; and *Ricinodendron heudelotii-Cephalosphaera usambarensis-Trichilia emetica* forest. In UMF the communities were *Parianari excelsa* forest, *Ricinodendron heudelotii-Newtonia buchanani-Antiaris toxicaria* forest, and *Brachystegia speciformis-Burkea africana-Uvariodendron pyconophyllums* forest. These communities correlated to a range of edaphic factors. The communities of ANR responded to sand, loamy sand, and sandy clay soil types, while in UMF the communities correlated with sandy loam and loamy sand soil types. All communities correlated with acidic soils in ANR and UMF. Tree communities of ANR correlated with high soil organic carbon, whereas in UMF communities 1 and 4 are associated with low organic carbon than communities 2 and 3 (Tables 4 and 5).

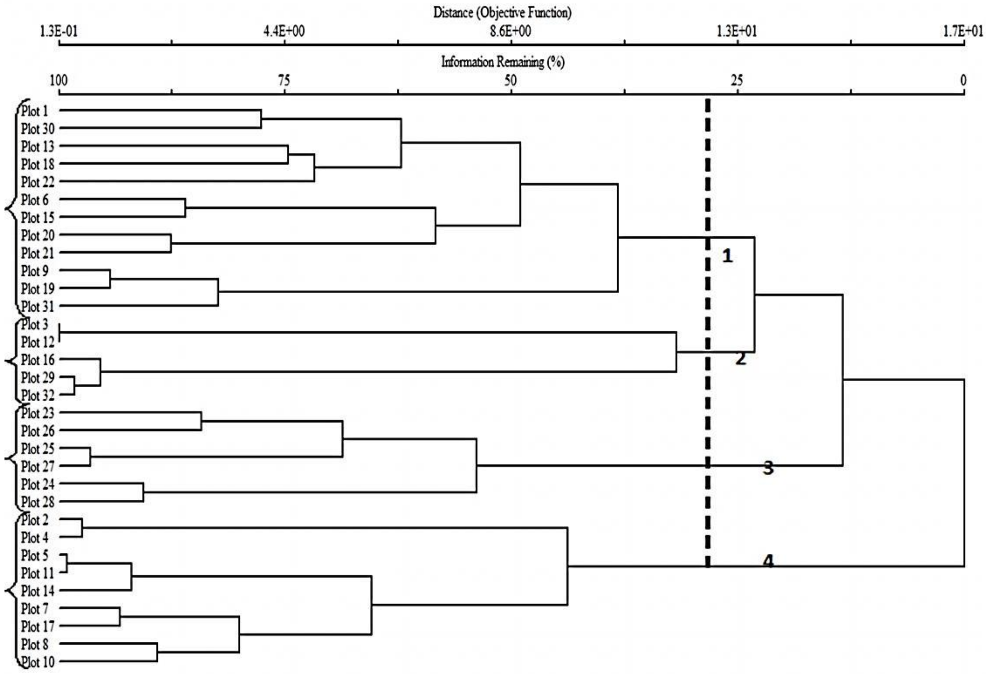

Fig. 4. Community dendrogram of Sørensen distances between plant communities along soil gradient in Amani Nature Reserve, Eastern Arc Mountains of Tanzania. Societies are base on species dominance estimated from the basal area.

3.3. Zonation of tree communities along climate and soil gradients

Zonation of plant communities and species associations were observed along climate and soil gradients in Usambara and Udzungwa Mountains (Ter Braak and Prentice, 2004). Along climate gradient, 4 and 5 distinc plant communities were determined in ANR and UMF, respectively. The plant communities for ANR were *Isoberlinia scheffleri-Bombax rhodognaphalon-Parinari excelsa* forest; *Synsepalum msolo-Newtonia buchananii-Tricalysia dregeana* forest; *Bridelia micrantha-Vitex doniana-Ricinodendron heudelotii* forest; and *Ricinodendron heudelotii-Cephalosphaera usambarensis-Trichilia emetica* forest while that of UMF were *Brachystegia bussei-Burkea africana-Uapaca kirkiana* forest; *Parianari excelsa-Pteleopsis myrtifolia-Tricalysia pallens* forest; *Ricinodendron heudelotii-Newtonia buchanani-Antiaris toxicaria* forest; Zonation of plant communities and species associations were observed along climate and soil gradients in Usambara and Udzungwa Mountains (Ter Braak and Prentice, 2004). Along climate gradient, 4 and 5 distinc plant communities were determined in ANR and UMF, respectively.

Table 4. Plant communities and species associations along soil gradient in Amani Nature Reserve, Eastern Arc Mountains of Tanzania.

Community	Associated species	Basal area (m²/ha)	B.D (g/cm³)	pH	Cts (%)	Css (%)	Soil type
Isoberlinia scheffleri-Bombax rhodognaphalon-Parinari excelsa forest 1	Isoberlinia scheffleri	164.6					
	Bombax rhodognaphalon	88.3	1.2	5.7	2.7	1.1	Sand
	Parinari excelsa	56.0					
	Terminalia sambesiaca	45.8					
	Milicia excelsa	44.4					
	Chrysophyllum perpulchrum	36.2					
	Cedrella odorata	26.5					
	Sorindeia madagascariensis	22.7					
	Barringtonia racemosa	22.1					
Synsepalum msolo-Newtonia buchananii-Tricalysia dregeana forest 2	Synsepalum msolo	47.5					
	Newtonia buchananii	43.4	1.1	5.4	3.4	1.0	Loamy sand
	Tricalysia dregeana	30.7					
	Funtumia africana	28.2					
	Syzygium guineense	25.1					
	Greenwayodendron suaveolens	11.1					
Bridelia micrantha-Vitex doniana-Ricinodendron heudelotii forest 3	Bridelia micrantha	15.6					
	Vitex doniana	12.4	1.1	6.0	3.4	1.4	Sandy clay
	Ricinodendron heudelotii	12.3					
	Dombeya shupangae	9.7					
	Lonchocarpus capassa	8.7					
	Erythrina abyssinica	7.9					
	Combretum molle	4.7					
Ricinodendron heudelotii- Cephalosphaera usambarensis- Trichilia emetica forest 4	Ricinodendron heudelotii	68.4					
	Cephalosphaera usambarensis	47.7	1.1	5.0	2.8	1.0	Loamy sand
	Trichilia emetica	37.7					
	Pterocarpus tinctorius	31.8					
	Maesopsis eminii	25.6					
	Milicia excelsa	24.9					
	Annickia kummeriae	20.5					
	Funtumia africana	18.8					
	Maesopsis eminii	16.6					

Note: Variables are average in three soil depths. Soil type is base on fractions with higher percentages; B.D = Bulk density; % Cts = Percentage organic carbon in topsoil; % Css = Percentage organic carbon in subsoil; Numbers 1, 2, 3 and 4 represent the different plant associations on Fig. 4.

Table 5. Plant communities and species associations along soil gradient in the Udzungwa Mountains, Eastern Arc Mountains of Tanzania.

Community	Associated species	Basal area (m²/ha)	B.D (g/cm³)	pH	Cts (%)	Css (%)	Soil type
Parianari excelsa forest 1	*Parianari excelsa*	113.4					
	Tricalysia pallens	41.6	1.1	4.8	4.1	1.9	Sandy loam
	Brachystegia bussei	17.6					
	Tabernaemontana usambarensis	11.1					
	Burkea africana	4.9					
	Uapaca kirkiana	3.3					
	Ricinodendron heudelotii	218.4					
Ricinodendron heudelotii-Newtonia buchanani-Antiaris toxicaria forest 3	*Newtonia buchanani*	127.2					
	Antiaris toxicaria	109.5	1.0	4.9	3.0	1.5	Loamy sand
	Brachystegia boehmii	76.2					
	Brachystegia bussei	56.1					
	Treculia africana	54.7					
	Lettowianthus stellatus	35.9					
	Ekebergia capensis	27.2					
	Allophyllus rubifolius	22.9					
	Allanblackia stuhlmanii	21.3					
	Sorindeia madagascariensis	20.8					
	Macaranga capensis	19.3					
	Premna senensis	18.1					
Brachystegia speciformis-Burkea africana-Uvariodendron pyconophyllums forest 3	*Brachystegia spiciformis*	47.5					
	Burkea africana	8.5					
	Uvariodendron pyconophyllums	5.8	1.2	5.9	1.4	0.6	Sandy loam
	Pericopsis angolensis	5.4					
	Brachystegia boehmii	5.1					
	Terminalia sambesiaca	4.5					
	Diospyros zombensis	3.8					
	Lettowianthus stellatus	3.5					

Note: Variables are average in three soil depths. Soil type is based on fractions with higher percentages. B.D = Bulk density; % Cts = Percentage organic carbon in topsoil; % Css = Percentage organic carbon in subsoil. Numbers 1, 2, 3, and 4 represent the different plant associations in Fig. 5.

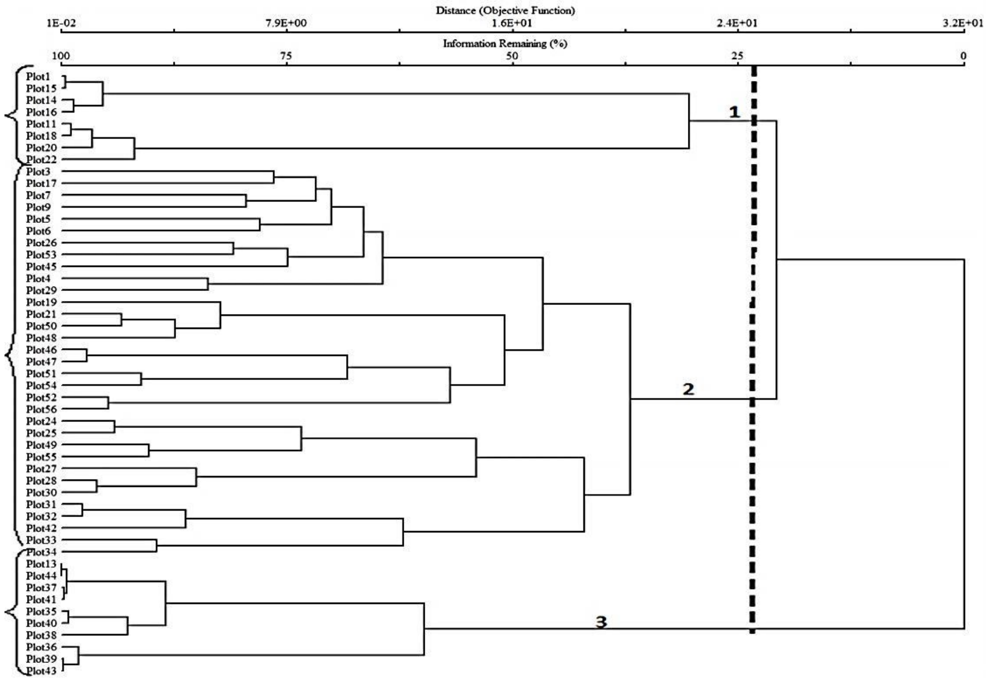

Fig. 5. Community dendrogram of Sørensen distances between plant communities along soil gradient in the Udzungwa Mountains, Arc Mountains of Tanzania. Communities are base on species dominance estimated from the basal area.

The plant communities for ANR were *Isoberlinia scheffleri-Bombax rhodognaphalon-Parinari excelsa* forest; *Synsepalum msolo-Newtonia buchananii-Tricalysia dregeana* forest; *Bridelia micrantha-Vitex doniana-Ricinodendron heudelotii* forest; and *Ricinodendron heudelotii-Cephalosphaera usambarensis-Trichilia emetica* forest while that of UMF were *Brachystegia bussei-Burkea africana-Uapaca kirkiana* forest; *Parianari excelsa-Pteleopsis myrtifolia-Tricalysia pallens* forest; *Ricinodendron heudelotii-Newtonia buchanani-Antiaris toxicaria* forest; *Brachystegia boehmii-Parinari excelsa-Holarrhena pubescens* forest; and *Brachystegia spiciformis-Burkea africana-Uvariodendron pyconophyllums* forest. Three tree communities that corresponded with low elevations/higher temperatures in ANR include *Isoberlinia scheffleri-Bombax rhodognaphalon-Parinari excelsa* and *Bridelia micrantha-Vitex doniana-Ricinodendron heudelotii. Synsepalum msolo-Newtonia buchananii-Tricalysia dregeana* and *Ricinodendron heudelotii-Cephalosphaera usambarensis-Trichilia emetica* corresponded to higher elevations/lower temperature. Similarly, two communities occurred at low elevations, two at mid-elevations, and one community at higher elevations in UMF. *Brachystegia bussei-Burkea africana-Uapaca kirkiana* and *Brachystegia spiciformis-Burkea africana-Uvariodendron pyconophyllums* forests corresponded to lower elevations/higher temperature in UMF. The communities at lower elevation consist of typical Miombo species commonly found in the lowland forests (lower slopes) of the UMF. *Parianari excelsa-Pteleopsis myrtifolia-Tricalysia pallens* and *Brachystegia boehmii-Parinari excelsa-Holarrhena pubescens* forests corresponded to mid-elevations, whereas *Ricinodendron heudelotii-Newtonia buchanani-Antiaris toxicaria* forest corresponded to higher elevations/lower temperature.

Many studies have reported changes in species diversity and composition and composition in the EAMs (Lovett, 1996; Ter Steege et al., 2006). The present study documents the existence of distinct communities along with climate and edaphic gradients. Other studies have reported continuous patterns of tree communities (Lovett, 1998); however, the results were not conclusive because there was no empirical data on environmental variables apart from elevation. Distinct communities can also be observed in structurally high complex, multilayered tropical montane forest communities (Hemp, 2006) as a function of altitude and factors related to altitude, such as water availability (Muenchow et al., 2013). The elevational zonation of vascular plants (trees, shrubs, epiphytes, lianas, and herbs) in Mt was observed. Kilimanjaro correlated strongly with altitude and temperature, whereby rainfall was found to influence epiphyte zonation greatly. Discrete communities were also observed in Andean tropical rain forests in a study assessing elevational zonation of cryptogam communities using the distribution of pteridophytes along elevational gradients in Bolivia, as well as lichens and bryophytes located in Colombia and Peru (Kessler, 2001; Parmentier et al., 2007).

Zonation of plant communities was noted along the soil gradient. In ANR, the plant communities were *Isoberlinia scheffleri-Bombax rhodognaphalon-Parinari excelsa* forest; *Synsepalum msolo-Newtonia buchananii-Tricalysia dregeana* forest; *Bridelia micrantha-Vitex doniana-Ricinodendron heudelotii* forest; and *Ricinodendron heudelotii-Cephalosphaera usambarensis-Trichilia emetica* forest while the was composed of *Parianari excelsa* forest, *Ricinodendron heudelotii-Newtonia buchanani-Antiaris toxicaria* forest, and *Brachystegia speciformis-Burkea africana-Uvariodendron pyconophyllums* forests. These communities correlated to a range of edaphic factors. The communities of ANR responded to sand, loamy sand, and sandy clay soil types, while in UMF the communities correlated with sandy loam and loamy sand soil types. All communities correlated with acidic soils in ANR and UMF. Tree communities of ANR correlated with high soil organic carbon whereas in UMF community 1 and 4 correlated with low organic carbon than community 2 and 3. Soil acisdity was also reported to have significant influence in zonation of vascular plants in Mt. Kilimanjaro (Hemp, 2006). Edaphic factors may filter the occurrence of plant species and communities by promoting or limiting plant growth. Thus plant communities may respond uniquely to both positive and negative (environmental stress) edaphic gradients forming distinct communities (zonation). Similar studies have indicated the edaphic influence (mainly soil acidity and texture) in partioning of plant communities in the EAMs. In a study conducted along the hyper-arid coast in the most diverse fog oasis in the Peruvian desert, soil texture and salinity accounted for 88% contrary to more humid tropical ecosystems where soil nutrients appear to be more important (Muenchow et al., 2013).

4. Conclusion

This study develops the understandings regarding plant community distribution in EAMs and other tropical ecosystems. Variation findings reported in some of the previous studies might be due to different sampling approaches and variables (environmental factors) used in the analysis.

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