



Faculty of Applied Ecology and Agricultural Sciences

Julius Vincent Lasway

Master thesis

Effect of altitude on woody vegetation along slopes of a  
volcanic, tropical mountain

Master in Applied Ecology

(June 2017)

---

28<sup>th</sup> APRIL '17

Date

EVENSTAD

Place



Signature

I agree that this thesis is for loan in the library

YES  NO

I agree that this thesis is open accessible in Brage

YES  NO

## Abstract

This study was initiated to investigate the effects of altitude on woody vegetation on the eastern slopes of Mount Meru, Tanzania. Changes in vegetation along altitudinal gradients are related to climate factors, soil quality and biotic factors. Changes in vegetation composition may or may not correspond with changes in species richness and diversity. Altitude may also affect woody plant structure, such as tree height and canopy cover. Based on studies from other East African mountains, I hypothesized that community composition of woody plants changes distinctly with altitude. I also hypothesized that species richness and diversity of woody plants, canopy cover and tree height decrease with altitude.

To test these hypotheses, I carried out a detailed vegetation survey in 44 plots of 10 meters by 10 meters, located in five transects ranging from 1600 to 3400 meters above sea level along the eastern slope of Mount Meru in Arusha National Park, Tanzania. I measured species abundance, tree height and canopy cover. I then analyzed changes in woody vegetation community composition, species richness, diversity, height and canopy cover in relation to altitude using multivariate analysis, and linear and generalized linear models.

Woody community vegetation composition changed distinctly with altitude. I identified three vegetation communities or vegetation zones; *Bersama abyssinica-Vepris simplicifolia*, *Hagenia abyssinica-Hypericum revolutum* and *Erica arborea*. Also I found that species richness and diversity, tree height and canopy cover decreased with increasing altitude. This was most likely caused by a combination of a decrease in atmospheric pressure, temperature, precipitation, competition and soil depth and an increase in solar radiation and wind speed with altitude.

This study describes three vegetation zones on the eastern part of Mount Meru, and show how vegetation composition and structure changes with altitude, which was previously poorly studied in this area. Therefore the information obtained from this study can act as baseline information for future studies. I therefore invite researchers to conduct studies on vegetation, plant species and climate change in the area.

---

 CONTENTS

<b>ABSTRACT.....</b>	<b>3</b>
<b>1. INTRODUCTION .....</b>	<b>6</b>
<b>2. METHODS.....</b>	<b>9</b>
2.1 STUDY AREA DESCRIPTION .....	9
2.2 LAND USE HISTORY OF THE STUDY AREA .....	9
2.3 STUDY DESIGN AND DATA COLLECTION .....	12
2.4 DATA ANALYSES .....	14
<b>3. RESULTS.....</b>	<b>16</b>
3.1 IDENTIFYING WOODY PLANT COMMUNITY .....	16
3.1.1 <i>Bersama abyssinica - Vepris simplicifolia</i> woodland plant community.....	16
3.1.2 <i>Hagenia abyssinica - Hypericum revolutum</i> woodland plant community.....	16
3.1.3 <i>Erica arborea</i> shrubland plant community .....	17
3.1.4 <i>Associating plant communities with altitude</i> .....	17
3.2 SPECIES RICHNESS, DIVERSITY, CANOPY COVER AND TREE HEIGHT .....	20
<b>4. DISCUSSION.....</b>	<b>23</b>
4.1 WOODY PLANT COMMUNITIES OF MOUNT MERU .....	23
4.1.1 <i>Bersama abyssinica - Vepris simplicifolia</i> .....	23
4.1.2 <i>Hagenia abyssinica-Hypericum revolutum</i> .....	24
4.1.3 <i>Erica arborea shrubland community</i> .....	25
4.2 SPECIES RICHNESS AND DIVERSITY .....	27
4.3 TREE HEIGHT VARIATION WITH ALTITUDE.....	28
4.4 CANOPY COVER VARIATION WITH ALTITUDE.....	30
4.5 MANAGEMENT IMPLICATIONS.....	31
4.6 CONCLUSION.....	31

---

<b>5. ACKNOWLEDGEMENTS .....</b>	<b>32</b>
<b>6. REFERENCE .....</b>	<b>33</b>

# 1. INTRODUCTION

Mountains cover about 25% of the earth's land surface, hosting at least one third of the terrestrial plant species (Körner 2007). In mountainous areas, vegetation composition, floristic diversity and forest structure change with increasing altitude (Grytnes & Beaman 2006; Guo *et al.* 2013; Pedroni, Eisenlohr & Oliveira-Filho 2013). These changes in vegetation are influenced by altitudinal gradients related to a number of abiotic factors, including atmospheric pressure, air temperature, humidity, precipitation, solar radiation and soil quality (Körner 2007; McCain 2010). Understanding how vegetation composition vary along altitudinal gradients is important for management and conservation of species diversity in a world that becomes increasingly warmer due to human impact on climate (Grytnes 2003). Climate change has been associated with changes in species distribution and composition with altitude (Lenoir *et al.* 2008). It has been shown that global warming results in a significant upward shift in species along altitudinal gradients, particularly for species distributed in mountain habitats (Kelly & Goulden 2008; Lenoir *et al.* 2008). Knowledge about this variation will facilitate protection and management of rare and threatened species, hence maintaining ecological patterns and ecosystem services (d'Arge *et al.* 1997).

Abiotic factors change with altitude which in turn affect vegetation composition and structure (Körner 2007). For every one hundred meter gain in altitude, atmospheric pressure declines by approximately ~ 1.1% (Körner 2007). Air temperature decreases on average with 0.6 °C for each one hundred meter increase in altitude (Barry 1992). Reduction in ambient air temperature reduces the humidity (saturated vapor pressure present in the atmosphere) (Barry 1992). Solar radiation increases with elevated altitude because of reduced atmospheric turbidity with altitude (Barry 2008). Cloud cover increases with elevation until the cloud zone often at between 1200 and 2500 m (Stadtmüller 1987), after which it decreases drastically. Precipitation tends to follow the clouds. Thus the most common precipitation pattern is an increase with altitude for example for mountains in arid and temperate latitudes (McCain & Grytnes 2010). Tropical mountains show extra variation in precipitation trends, and display decreasing trends, unimodal or bimodal trends with high precipitation at the cloud zone at mid elevations (Barry 2008). The interaction among precipitation, solar radiation, temperature and cloud cover determines the productivity in addition to soil depth and quality. As with precipitation, altitudinal trends in productivity

---

may vary considerably among mountains (McCain & Grytnes 2010). Wind speed does not always follow the altitudinal gradients, but mostly increases with altitude (Barry 2008).

The factors mentioned above, together with biotic factors such as competition, habitat heterogeneity and complexity, dispersal and establishment influence vegetation composition patterns along altitudinal gradients (McCain & Grytnes 2010). However, there is no clear pattern which shows how biotic factors vary with altitude (McCain & Grytnes 2010). Hedberg (1951) observed vegetation composition to vary between different sides of the same mountain at equivalent elevations. The side of the mountain receiving moisture-laden winds has different vegetation composition compared to the leeward side in rain shadow (Lawton 1982).

Altitudinal vegetation zonation describes the natural vegetation layering that occurs at distinct altitudes due to varying climatic conditions and soil quality (Hemp 2006a). Several studies conducted in East African mountains suggests presence of vegetation zones or alternatively referred to as vegetation belts, which are altitudinal related discontinuous variations in vegetation composition and structure (Hedberg 1951; Hemp 2006b). Hedberg (1951) identified three main vegetation belts in East African mountains: from above, the alpine belt, the ericaceous belt and the montane forest belt which was confirmed by Lundgren and Lundgren (1972). Hedberg (1951) further classified the montane forest zone based on moisture availability into montane rain forest, bamboo zone and *Hagenia-Hypericum* zone. Vegetation zones occupy different altitudes in different mountains. For example the montane forest zone was located between: 2150 and 3200 m on Mt. Elgon, 2000 and 3450 on Mt. Kenya, 1900 and 2950 on Mt. Kilimanjaro and 1700 to 3100 m on Mt. Meru. The ericaceous zone occurs between: 3200 and 3550 m on Mt. Elgon, 3400 and 3600 m on Mt. Kenya, 3250 and 4000 on Mt. Kilimanjaro and 3100 to 3600 m on Mt. Meru. The afro-alpine zone was found between: 3550 and 4321 m on Mt. Elgon, 3600 and 5199 m on Mt. Kenya, 4000 m until snow cover on Mt. Kilimanjaro and between 3600 and 4562 m on Mt. Meru. Hedberg (1951) also mentioned presence of a moorland vegetation belt on Mt. Kilimanjaro between 2900 to around 4000 m a.s.l. Chapman and White (1970) suggested an alternative classification of montane forest in East Africa into montane forest “sensu stricto” and seasonal rain forest. This was accepted by Coetzee (1978) who said this classification was based not only on moisture but also on floristic composition, physiognomy and ecology. However, grouping montane forest in two groups as suggested by Chapman and White

(1970) disregards the great variation in physiognomy and floristic composition which was recognized by Hedbergs' (1951) classification.

Hamilton (1975) observed tropical mountain forest vegetation forms a continuum and not a zonation as suggested by Hedberg (1951). A continuum means that the forest vegetation shows a slow continuous change over altitudinal gradients and therefore does not form distinct vegetation zones as observed by Hedberg (1951).

Lack of knowledge about vegetation composition and distribution patterns along altitudinal gradients, results in challenges for species conservation and management (Hunter & Yonzon 1993). The study of these relationships is therefore important for conservation and management of species diversity (Grytnes 2003). A review study of Rahbek (1995) has shown that variation in plant species richness and diversity with altitude is a result of decreased temperature, atmospheric pressure, precipitation, humidity, and productivity. However the pattern in changing species richness with increasing altitude may be either a monotonic decrease or a hump shaped pattern (Odland & Birks 1999; Grytnes & Beaman 2006). Some studies conducted in tropical mountains of south Ecuador and Costa Rica have shown that tree height decreased with altitude as a result of increased wind speed, decreased soil depth and decreased precipitation (Lieberman *et al.* 1996; Coomes & Allen 2007; Körner 2007; Moser 2008). Also, canopy cover has been shown to decrease with elevation as a result of increased sunlight and wind speed (Bianchini, Pimenta & dos Santos 2001).

In East African mountains, variation with altitude in vegetation community composition, species richness and diversity, canopy cover and tree height is as little known as the factors causing the variation. Therefore, in this thesis, I attempt to elucidate the effects of an altitudinal gradient on woody vegetation in the eastern slopes of Mt. Meru. The results of this study may act as a baseline for further studies in the area. I hypothesize that, i) woody plant community composition changes distinctly with altitude, ii) species richness of woody plants decreases with altitude, iii) the Shannon-Wiener (S-W) diversity index for woody plant species decreases with altitude, iv) woody plant canopy cover decreases with altitude and iv) tree height decreases with altitude.



## 2. METHODS

### 2.1 Study area description

This study was conducted on the eastern slopes of Mt. Meru at 36°45' E-3°15' S in Arusha National Park, Tanzania (Figure 1). The park covers an area of 552 km<sup>2</sup> (TANAPA 2017). The habitats of Arusha National Park, previous Mt. Meru Game Reserve, include an evergreen forest, shrublands, wetlands and glades (Mangubuli & Lyamuya 1988). The area has two rainy seasons: a long rainy season between late February or early March and May and the short rainy season between November and December. Average annual rainfall ranges geographically between 1300 and 2400 mm. The annual mean maximum temperature (hottest season) is 25.4°C between January and February and minimum temperature (cold season) is 12.8°C between June and August (Kahana, Malan & Sylvina 2015). Temperature and rainfall information are not necessarily valid for the upper slopes. The upper parts, even in the forest, have more of a day climate than a seasonal climate, meaning that every night it gets close to freezing temperatures while the days get warm (Hedberg & Hedberg 1979; Sarmiento 1986). This is a climate that is very harsh for plants and forces a lot of specific adaptations (Hedberg 1951). The soil of the area originates from volcanic activities of Mt. Meru (Razzetti & Msuya 2002).

### 2.2 Land use history of the study area

Mt. Meru is a relatively young volcanic mountain formed during the late Pleistocene time period, around 1.8 million to 10,000 years ago (Lundgren & Lundgren 1972). When the Europeans arrived in the late nineteenth century they found the lowland areas below the mountain inhabited by Meru and Maasai tribes (Lundgren & Lundgren 1972). The former are mixed farmers and the latter are mainly nomadic livestock keepers (Lawson *et al.* 2014). The last evidence of volcanic eruption was noted in the year 1910. The evidence of fires, perhaps natural, in the ericaceous zone and mid altitude between 2600 and 2800 m.a.s.l of Mt. Meru was noted in the late 1940's by Hedberg (1951). At different times, parts of the mountain have been subjected to different management regimes. Early in the twentieth century, the forest was set aside as a forest protection reserves and was later declared as a

game reserve in 1946 (Lundgren & Lundgren 1972). During 1950's, Europeans and Kikuyu refugees cultivated the Eastern slopes of Mt. Meru for short periods with pyrethrum, *Chrysanthemum cinerariaefolium* and *C. coccineum*; for manufacturing of insecticide. The area was upgraded to the National Park in 1960 and the whole Eastern side of the mountain was included in Arusha National Park (Lundgren & Lundgren 1972).

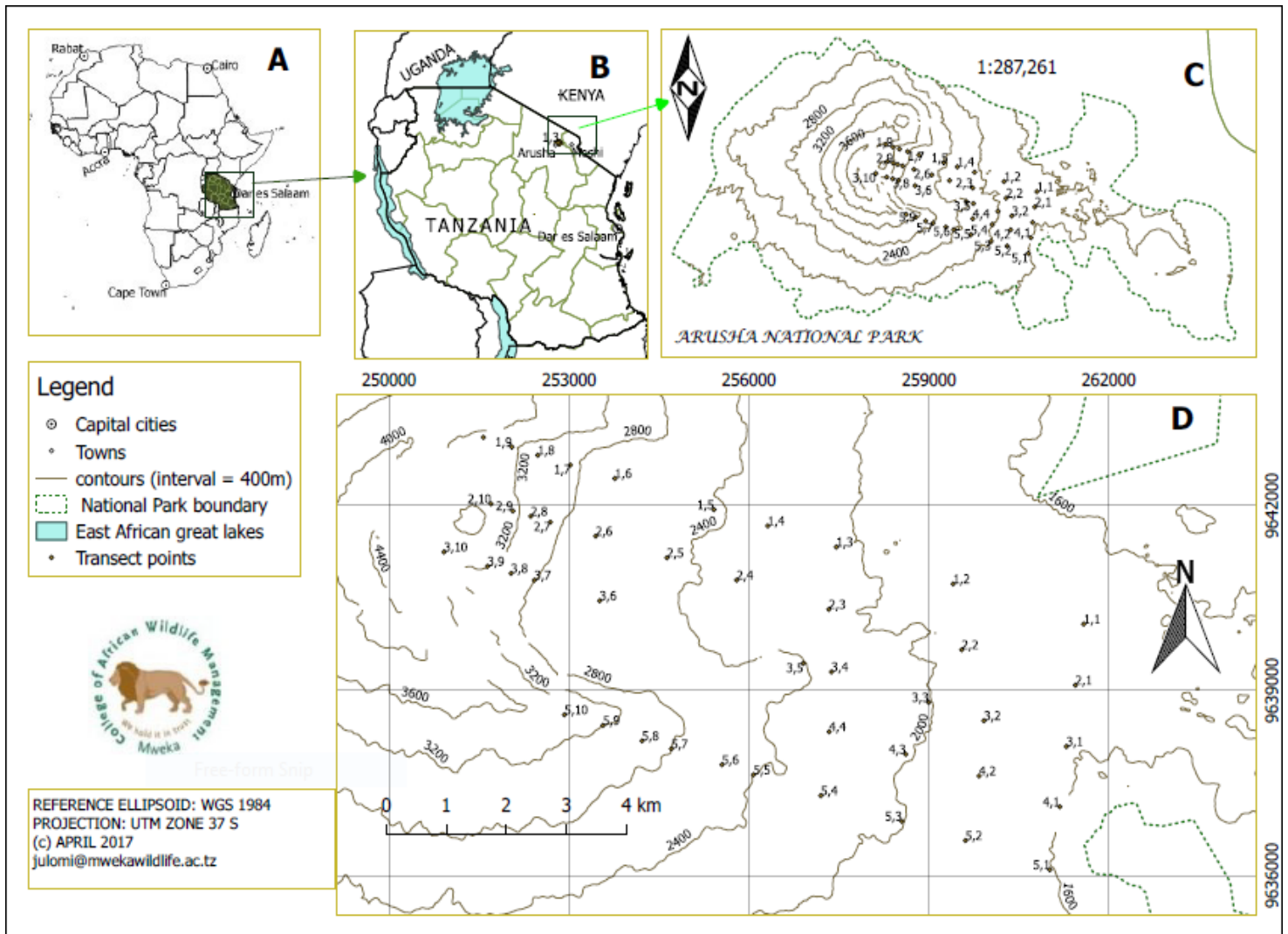


Figure 1. C and D. Map of Arusha National Park showing distribution of plots on transects along the eastern slopes of Mt. Meru. The first number stands for the transect and the second number stand for the plots. E.g. "2,7" means seventh plot from low to high altitude in the second transect. A and B shows the African continent and Tanzania respectively

## 2.3 Study design and data collection

I carried out field data collection from early February to early April 2016 through plot-based sampling. Since altitude was a primary predictor, I made five transects after looking at a map (scale 1:500,000) to find transects with relatively long continuous slope with no variation in aspect. I laid out transects systematically, with approximately 1 km distance between each transect, from the lowlands escalating west to the mountains, keeping within the borders of the National Park.

I drew transect lines from the lowest altitude, 1600 meters above sea level (m.a.s.l), to the highest altitude, 3400 m.a.s.l of the study area. The first point at the lowest altitude was 1600 m.a.s.l obtained by using a Global Positioning System (GPS). To obviate overlapping of the transect lines, all transects were laid out along a constant bearing among transects of 287 degrees from the first point of the transect at 1600 m.a.s.l. At every 200 m increase in altitude, starting at 1600 m, a quadratic plot of 10 m  $\times$  10 m was positioned on the north side of the transect along the transect line. To make sure the plots were of the same size, the diagonal of 14.14 m was measured between two opposite corners of the plot using a tape-measure. When the plot fell on unsuitable places, such as, human influenced areas, huts, viewpoints or rivers, I went 50 m west to identify a new plot. The number of plots in each transect were 10 to make the total number of 50 plots. During data collection, I succeeded in reaching only 44 plots, 40 plots in the four transects (1, 2, 3 and 5) and 4 plots in the transect 4, because the terrain was too steep to access the plots.

In each plot, I recorded both plot variables, date, transect number, plot number, latitude, longitude, and altitude as measured by GPS and tree variables (as described below). Every tree in the plot with a height greater than 1 m was recorded and identified to the species level following Turrill and Milne-Redhead (1952). Species not identified in the field were taken to the National Herbarium of Tanzania (NHT) located in Arusha city for identification. To make this possible, they should have fruits or flowers and leaves. For this study, I defined a woody plant as any plant with height more than 1 m above the ground with a single or multiple stems (no distinction between a tree and a shrub).

For each tree, two projections of canopy diameters (the longest and the perpendicular one) were measured up to the closest cm, using a tape measure. Height of the trees were measured in meters using a measuring pole for small trees (less than 5 m high) and a Suunto clinometer for large trees (more than 5 m high) from the ground to the top of the highest living shoot.

I used the Shannon Wiener Index (Magurran 2013) as an index of species diversity, calculated using the formula:

$$H' = - \sum_{i=1}^R p_i \ln p_i$$

Where  $H'$  is the index of species diversity,  $p_i$  is the proportion of total sample belonging to the  $i$ th species and  $R$  is the total number of species per plot (Krebs 1989). I decided to use this index since both species richness (number of species present) and species abundance are taken into account. However it assumes all species that are present in the plot are also present in the records.

I calculated canopy cover by assuming the projection of the canopy was a circle. Therefore, for each individual plant I calculated an average diameter,  $D$  from the longest and the perpendicular diameter. The obtained average diameter was used to calculate the canopy area based on the formula ( $A = (\pi/4) \times D^2$ ), where  $A$  is a canopy cover,  $\pi$  is a constant, 3.14 and  $D$  is an average diameter. The area calculated for each individual plant in the plot was summed to get a total canopy cover per plot which was later used in statistical analysis to relate altitude to canopy cover. Tree height per plot was calculated as the average height of all individuals in a plot.

---

## 2.4 Data Analyses

To analyze the variation in woody plant community composition with altitude in hypothesis i), I performed multivariate analyses (ordinations) using CANOCO version 5.0 (Šmilauer & Lepš 2014). This program creates ordination axes displaying the maximum variation in species data and creates graphs with CANODRAW to visualize the variation. Plots shown in close proximity to each other have similar plant species composition whilst plots far apart have dissimilar species composition. Ordination techniques can summarize complex multivariate data by producing graphs showing clusters of samples with similar species composition that may be interpreted as communities. Moreover ordination can also link species data with environmental variables in biplots, or show samples and species (Gauch 1982). The communities identified were named based on dominant species or two highly abundant species. Dominant species were defined as the most abundant species with  $\geq 50\%$  of all trees in the community and highly abundant species as species with  $< 50 \geq 20\%$  of all trees in the community.

Unimodal response models assume that species abundance has been measured along long environmental gradients with bell shaped species responses to environmental variables. Each species has usually the highest abundance at an optimal value of each environmental variable. Linear response models assume a linear relationship between species performance and environmental variables with generally a short gradient (Šmilauer & Lepš 2014). I performed Detrended Correspondence Analysis (DCA) which showed the length of axis 1 to be 10.2 standard deviations. This value is higher than the threshold value of about 4, and therefore suggests a long gradient and a unimodal species distribution (Šmilauer & Lepš 2014). Hence I chose to use unimodal models.

Then I used unconstrained ordination, Correspondence Analysis (CA) to investigate if there were clusters with similar species composition (Šmilauer & Lepš 2014). Here altitude was added in the diagram after ordination. This was followed by running constrained weighted averaging ordination, Canonical Correspondence Analysis (CCA) to relate species data statistically to the environmental variable altitude. Statistical significance of the relationship between the response (species composition) and explanatory variable (altitude), was evaluated using a Monte Carlo permutation test with 499 permutations (default). The significance of the test was assessed from the  $p$  value obtained ( $p < 0.05$ ).

I used a generalized linear models (GLM) in the program R 3.2.2 (<http://cran.r-project.org/>) (McCullagh & Nelder 1989) for hypothesis ii) to relate woody plant species richness to altitude (explanatory variable). The response variable species richness takes the form of discrete data (counts) and hence has a Poisson distribution (McCullagh & Nelder 1989), which requires a logarithmic link function.

For hypothesis iii) to v) all responses were continuous, therefore I used linear models in R to analyze the relationship between response variables and altitude. Linear model assumptions such as linearity, independence of errors, equal variance of errors, and normality were checked (Crawley 2007). I had a few outliers, two high values for canopy cover and three low values of S-W diversity index. To test if the outliers affected the analysis, I carried out the analysis with and without the outliers, and compared the results. The *p value* obtained from the model summary *F* test was used to evaluate if there was a significant relationship ( $p < 0.05$ ) with altitude.

---

## 3. RESULTS

I registered totally 447 woody plant individuals from 36 different plant species in 44 sample plots ranging from 1600 m to 3400 m altitude.

### 3.1 Identifying woody plant community

Correspondence Analysis (CA) results revealed three distinct clusters of samples which represent three woody plant communities in the study area (Figure 2). The communities were named after the dominant species, or two highly abundant species. The plant communities identified were Community 1, *Bersama abyssinica*-*Vepris simplicifolia* woodland, Community 2, *Hagenia abyssinica*-*Hypericum revolutum* woodland and Community 3, *Erica arborea* shrubland (Figure 2). The three different woody plant communities identified by Correspondence Analysis (CA) were characterized by differences in altitude, species composition, species diversity and species richness (Table 1), as described in the following paragraphs.

#### 3.1.1 *Bersama abyssinica* - *Vepris simplicifolia* woodland plant community

This community was found in 24 different sample plots, and was therefore the most common in this study (Figure 2). Individual species found in high abundance included, *Bersama abyssinica* (21.5% of all individuals) followed by *Vepris simplicifolia* (20.1% of individual plants). I counted about 10.3 individual trees per plot in this community (totally 246 individuals), with 24 in species richness and a diversity index of 1.1272 (Table 1). This community had a higher species richness and diversity than the other two communities (Table 1). The community was found at the lower altitude of the study area, between 1600 and 2400 m.a.s.l

#### 3.1.2 *Hagenia abyssinica* - *Hypericum revolutum* woodland plant community

This community was characterized by two highly abundant species occurring in 13 different sample plots. *Hypericum revolutum* and *Hagenia abyssinica* were highly abundant woody plants found in this community (Table 1). *Hypericum revolutum* was represented by 23.9% of all individuals followed by *Hagenia abyssinica*, 22.4% of individuals. I counted totally



134 individuals in this community, about 10.3 individuals per plot, with 9 in species richness and a diversity index of 0.9775 (Table 1). This community was found in 12 sample plots at higher altitudes (2800 to 3200 m.a.s.l) and 1 sample plot at the highest altitude (3400 m.a.s.l) (Figure 2).

### **3.1.3 *Erica arborea* shrubland plant community**

This community was characterized by *Erica arborea* as the dominant species, appearing in all sample plots (Table 1). *Erica arborea* represented 55% of all woody plant individuals in this community (Table 1). The community had plants derived from 7 sample plots, about 9.6 individuals per plots (Figure 2); four sample plots with 37 individuals at the mid altitude (2600 m.a.s.l) and three sample plots with 30 individuals at the highest altitude (3400 m.a.s.l). Species richness in this community was 8 and diversity index of 0.7817. The community had a lower species richness and diversity than the other two communities (Table 1).

### **3.1.4 Associating plant communities with altitude**

Results from forward selection using CCA with a Monte Carlo permutation test showed that altitude was significantly correlated with variation in species data ( $F = 4.8$ ,  $p = 0.002$ ). The explanatory variable (altitude) explained 10.2% of total variation in species composition.

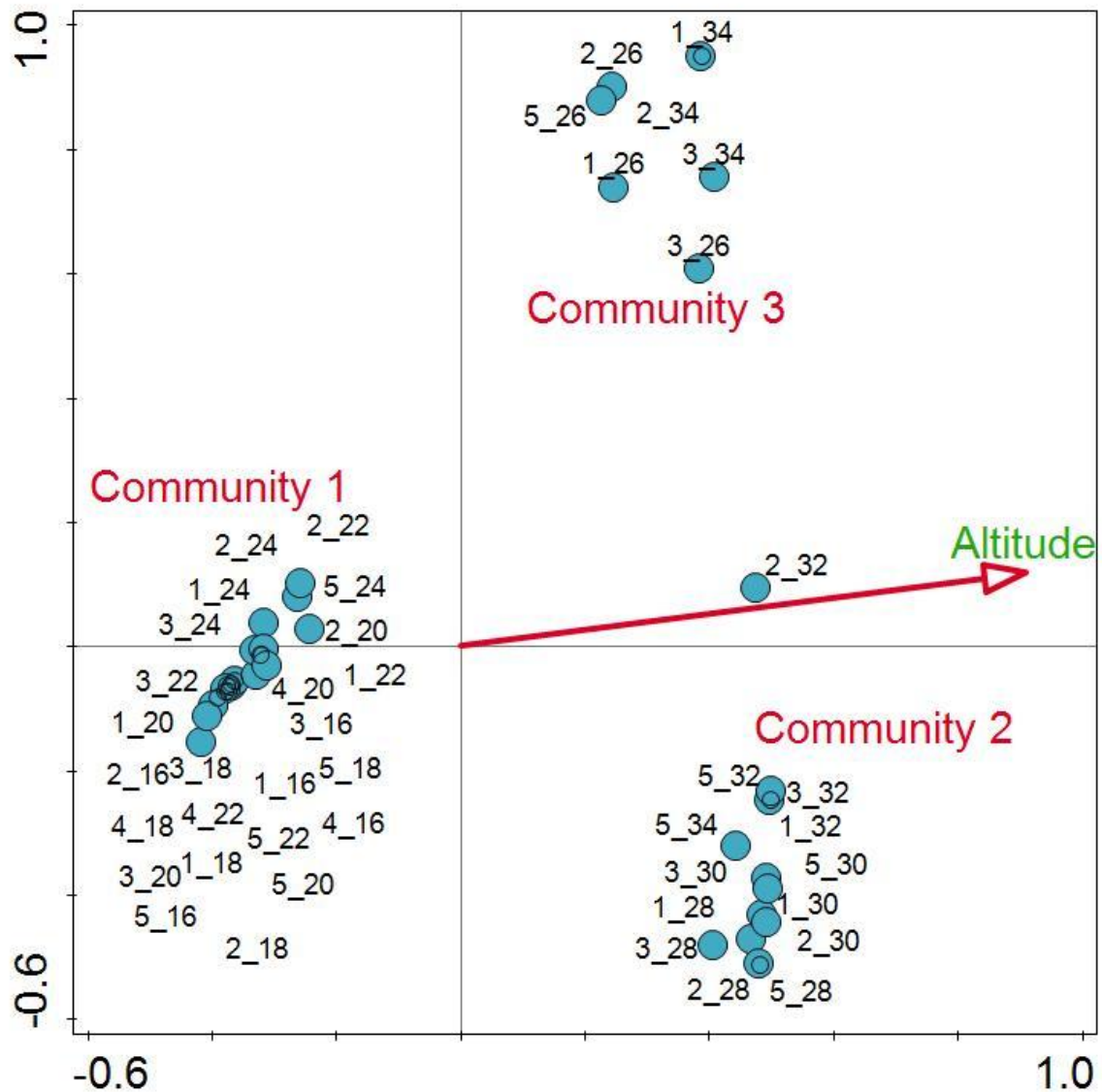


Figure 2. Biplot ordination diagram from Correspondence Analyses on Mt. Meru, Tanzania. Small blue circles represent the plots and the environmental variable, altitude, is represented by a red arrow. The plots are distributed based on their maximum variation in species composition. The first number in each plot refers to the transect number and the following two numbers are hundred meters altitude where the plot was positioned (E.g., "1\_16" means first transect plot positioned at sixteen hundred meter altitude). Community 1, 2 and 3 are *Bersama abyssinica*-*Vepris simplicifolia*, *Hagenia abyssinica*-*Hypericum revolutum* and *Erica arborea* woody plant community respectively.

Table 1. Characteristics of woodland plant communities identified from figure 2, including total number of individuals, altitude (m), species richness (sum of all plots), species diversity (average of all plots), number of plots, dominant species ( $\geq 50\%$  in all plots), highly abundant species ( $< 50 \geq 20\%$  in all plots) and other species from Mt. Meru, Tanzania.

	<i>Bersama abyssinica- Vepris simplicifolia</i>	<i>Hagenia abyssinica- Hypericum revolutum</i>	<i>Erica arborea</i>
<b>Total individuals</b>	246	134	67
<b>Altitude, m</b>	1600 - 2400	2800 - 3200	2600 and 3400
<b>Species richness</b>	24	9	8
<b>Species diversity</b>	1.1272	0.9775	0.7817
<b>Number of plots</b>	24	13	7
<b>Dominant species</b>	-	-	<i>Erica arborea</i> (55%)
<b>Abundant species</b>	<i>Bersama abyssinica</i> (21.5%) <i>Vepris simplicifolia</i> (20.1%)	<i>Hypericum revolutum</i> (23.9%) <i>Hagenia abyssinica</i> (22.4%)	-
<b>Other species</b>	<i>Albizia petersiana</i> <i>Casearia battiscombei</i> <i>Croton macrostachyus</i> <i>Dodonea viscosa</i> <i>Ekebergia capensis</i> <i>Euclea divinorum</i> <i>Juniperus procera</i> <i>Lepidotrichilia volkensii</i> <i>Lippia javanica</i> <i>Myrtus sp</i> <i>Nuxia congesta</i> <i>Olea africana</i> <i>Olea capensis</i> <i>Peddiea fischeri</i> <i>Podocarpus milanjanus</i> <i>Rauvolfia caffra</i> <i>Syzygium guineense</i> <i>Ritiginia spp</i> <i>Tabernaemontana ventricosa</i> <i>Trichilia emetica</i> <i>Turraea robusta</i> <i>Xymalos monospora</i>	<i>Agauria saticifolia</i> <i>Bersama abyssinica</i> <i>Crotalaria agatiflora</i> <i>Erica aborea</i> <i>Podocarpus africana</i> <i>Podocarpus milanjanus</i> <i>Stoebe kilimandscharica</i>	<i>Agauria saticifolia</i> <i>Hagenia abyssinica</i> <i>Juniperus procera</i> <i>Hypericum revolutum</i> <i>Myrsine africana</i> <i>Stoebe kilimandscharica</i> <i>Erica exelsa</i>

---

## 3.2 Species richness, diversity, canopy cover and tree height

Species richness showed a significant relation with altitude, where species richness decreased with increasing altitude ( $Z = 2.68$ ,  $dF = 43$ ,  $p < 0.001$ ,  $R^2 = 0.28$ ). with slope  $-0.0004 \pm 0.00014$  (Estimate  $\pm$  standard error on the log scale) (Figure 3 show the back transformed estimates). Similar to species richness, woody plant species diversity decreased with increasing altitude, ( $F_{1,39} = 5.3$ ,  $p = 0.0002$ ,  $R^2 = 0.278$ ) with slope  $-0.0003 \pm 0.00007$  (Estimate  $\pm$  standard error). Without outliers ( $F_{1,42} = 16.18$ ,  $p = 0.027$ ,  $R^2 = 0.120$ ) with slope  $-0.00016 \pm 0.00007$ (Estimate  $\pm$  standard error) (Figure 4).

Woody plant canopy cover decreased with increasing altitude ( $F_{1,42} = 47.44$ ,  $p < 0.001$ ,  $R^2 = 0.530$ ) with slope  $-0.077 \pm 0.01115$  (Estimate  $\pm$  standard error) (Figure 5). Without outliers ( $F_{1,40} = 82.44$ ,  $p < 0.001$ ,  $R^2 = 0.673$ ) with slope  $-0.059 \pm 0.0065$  (Estimate  $\pm$  standard error). Tree height also decreased with increasing altitude ( $F_{1,42} = 96.55$ ,  $p < 0.001$ ,  $R^2 = 0.697$ ) with slope  $-0.003 \pm 0.0003$ (Estimate  $\pm$  standard error) (Figure 6)

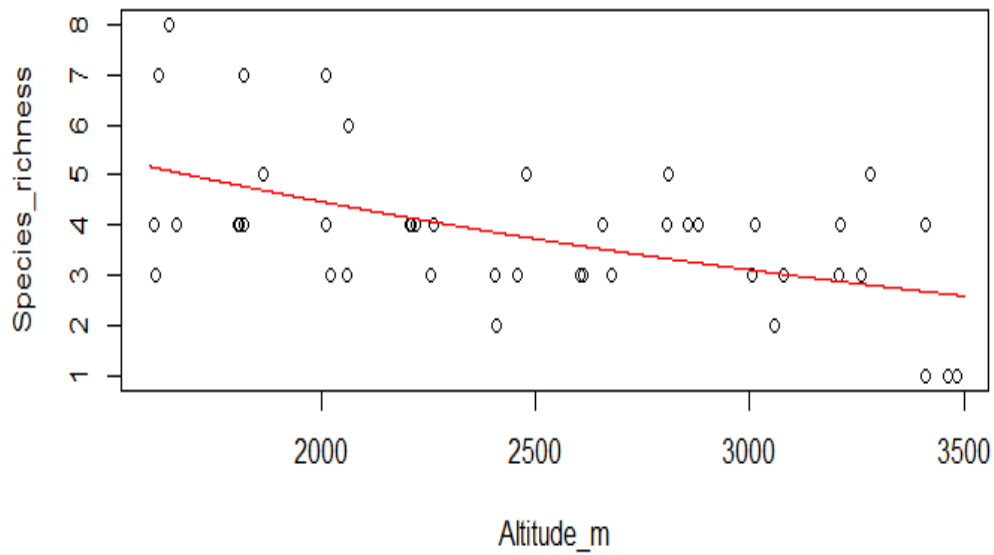


Figure 3. The relationship between altitude (m.a.s.l. = x axis) on Mt. Meru, Tanzania and woody plant species richness per plot, the fitted line based on back-transformed estimates from a generalized linear model.

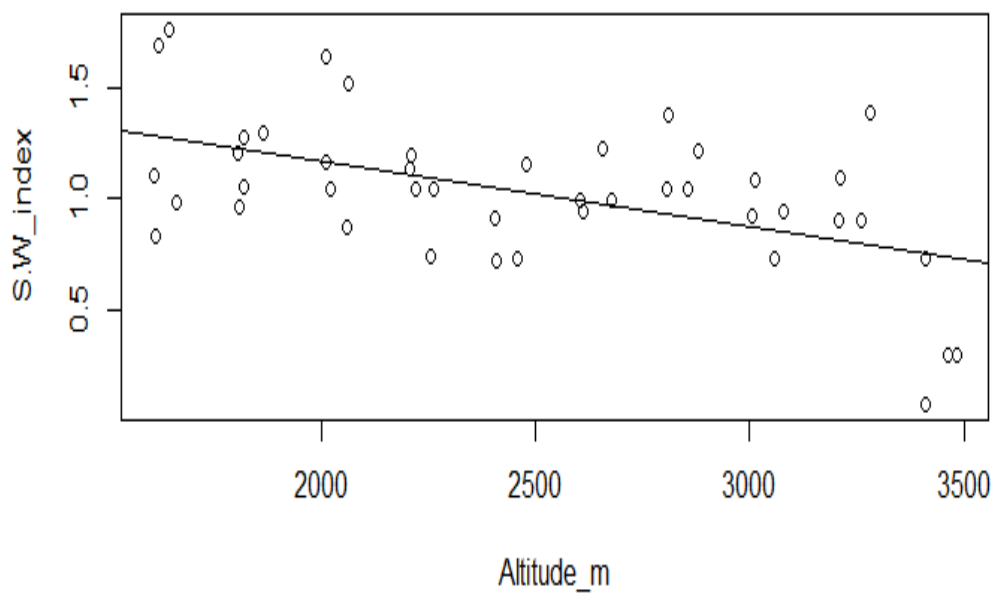


Figure 4. The relationship between altitude (m.a.s.l. = x axis) on Mt. Meru, Tanzania and Shannon-Weiner index of tree diversity per plot, the fitted line based on a linear model.

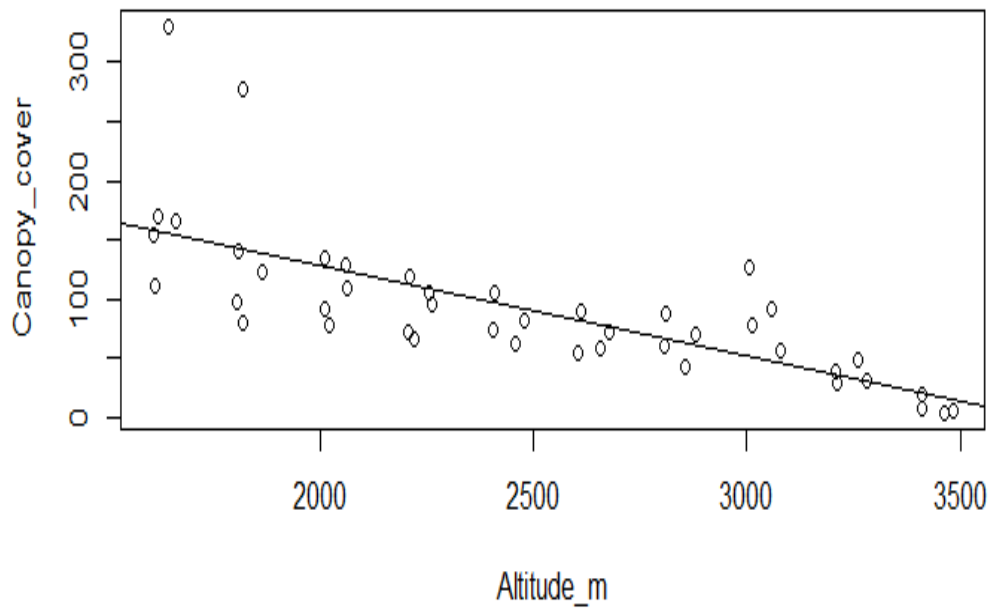


Figure 5. The relationship between altitude (m.a.s.l. = x axis) on Mt. Meru, Tanzania and sum canopy cover per plot measured in meter squared (m<sup>2</sup>), the fitted line based on a linear model.

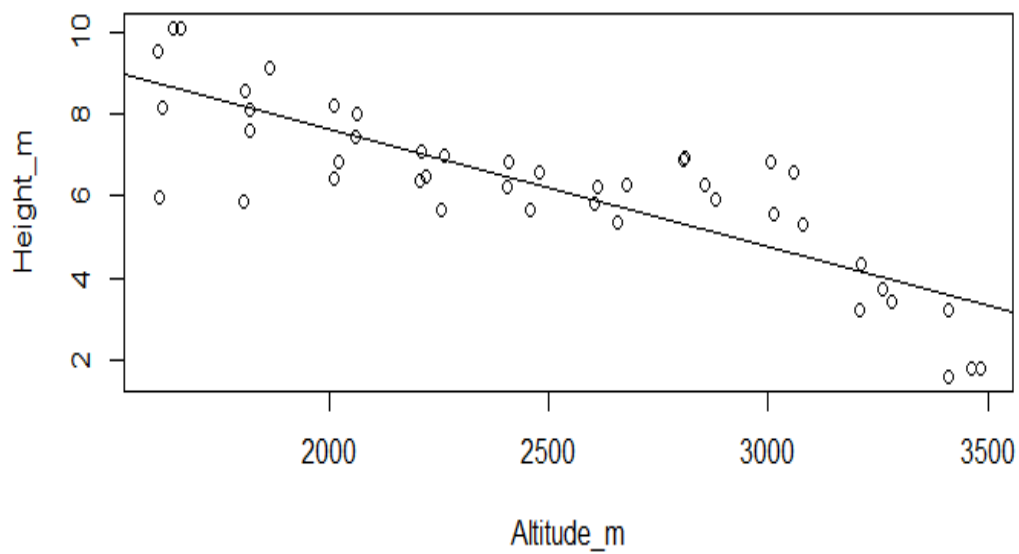


Figure 6. The relationship between altitude (m.a.s.l. = x axis) on Mt. Meru, Tanzania and average tree height in meters per plot, the fitted line based on a linear model.

## 4. DISCUSSION

This study identified three distinct vegetation communities distributed at different altitudes along the eastern part of Mt. Meru. This confirmed my prediction that woody plant community composition changes distinctly with altitude, and documents the presence of vegetation zones as it was described by Hedberg (1951) and not vegetation continuum as claimed by Hamilton (1975). The results also support my predictions that species richness, species diversity, tree height, and canopy cover decrease with increasing altitude.

### 4.1 Woody plant communities of Mount Meru

I identified three woody plant communities in the study area; *Bersama abyssinica-Vepris simplicifolia* woodland, *Hagenia abyssinica-Hypericum revolutum* woodland and *Erica arborea* shrubland communities. I called the *Erica arborea* community a shrubland since it fits well the definition of a shrubland as *Erica arborea* is a multiple stems plant with a relatively shorter height of 1 to 4 m (La Mantia *et al.* 2007). The identified woody plant communities varied distinctly in species composition and with altitude. The communities identified in this study, correspond to the ericaceous zone (at 2600 and 3400 m) and the two woodland communities correspond to the montane zone (between 1600 and 3200 m) which is slightly different from the observation of Hedberg (1951) and Bussmann (2006) from the same mountain. This will be discussed under each community below.

#### 4.1.1 *Bersama abyssinica - Vepris simplicifolia*

This community was located at the lower altitude of the study area between 1600 and 2400 m.a.s.l. The community lies within the montane forest of the study area as observed by Lundgren and Lundgren (1972). The tree species which I observed in this community were relatively tall and broad-leaved compared to the other two communities. This is the same as the observation made by Kitayama and Aiba (2002) and Hedberg (1951), they observed that the montane forest, particularly the lower montane forest belt is distinctly characterized by great numbers of broad-leaved evergreen trees. Tall trees and broad leaves are probably due to light competition adaptations. The occurrence of the two highly abundant species *Bersama abyssinica* and *Vepris simplicifolia* shows that the community is within the montane forest zone as Dharani (2002) describes in her book, "*Trees and shrubs of East*

---

*Africa*". She observed that these two species were distributed in wet and dry mountain forest of Tropical East Africa. The community had a higher species richness and diversity index than the other two communities. This may be because the community is found in the lower altitude of the study area and species richness and diversity decreases with increasing altitude. *Bersama abyssinica* is a broadleaved tree or shrub growing between 2 - 18 m tall. It is found in wet and dry montane and riparian forests, glades and forest-glade edges at altitudes between 1200 - 2400 m (Dharani 2002). *Vepris simplicifolia* is an evergreen tree species of East Africa which at maturity reaches the height of 4 - 10 m. It is widespread in both dry and wet forest at altitudes from 300 - 2300 m (Dharani 2002). I found the species within the same altitude as observed by Dharani (2002). All species which occurred in this community are indigenous to East Africa.

Other species I observed in this community includes *Podocarpus milanjanus*, *Olea capensis*, *Ekebergia capensis*, *Juniperus procera* and *Lepidotrichilia volkensii*. These species were also observed by Hedberg (1951). The species had changed names from Hedberg (1951) identification, *Olea hochstetteri*, *Ekebergia rueppelina*, *Trichilia volkensii* to *Olea capensis*, *Ekebergia capensis* and *Lepidotrichilia volkensii* respectively.

#### **4.1.2 *Hagenia abyssinica*-*Hypericum revolutum***

This community was composed of two highly abundant species, *Hagenia abyssinica* and *Hypericum revolutum*. The community was found in the upper montane forest between 2800 and 3200 m.a.s.l, below the ericaceous zone. This result is inconsistent with Hedberg (1951) who found no such distinct zone in eastern slopes of Mt. Meru. He found this zone only on the western slopes between 2550 and 3050 m, where *Hagenia abyssinica* seems to be the dominant forest tree throughout the belt. The vegetation change with time since Hedberg (1951) can be explained by climate change which cause local extinction (Cahill *et al.* 2012), or by other natural processes such as competition and browsing pressure. The area was upgraded to National Park in 1960, leading to high protection and management and therefore lower human impact on vegetation

This community was found in the upper montane forest belt, which is typically characterized by trees with twisted trunks, lower rainfall than the moist montane zone and presence of *Eleusine jaegeri* as understory grass (Niemelä & Pellikka 2004). Observation of *Hagenia abyssinica* between 2800 and 3200 m.a.s.l altitude is consistent with Dharani's (2002)



---

observations that the species occupies an altitude between 2400 and 3250 m in tropical mountains of East Africa. *Hagenia abyssinica* is a light-requiring species and therefore does not regenerate under dense canopy. It is usually dominant in the higher montane forest where light is not a problem (Hamilton 1982). The observation of Hamilton (1982) is also consistent with my results, since the species was found in upper montane forest where light is plentiful. The species was found together with *Hypericum revolutum*, an indigenous shrub or small tree that grows between 1 and 10 m high. It occurs in the upper montane forest at between 2100 and 3250 m.a.s.l (Dharani 2002). The plant species is a characteristic of afro-montane vegetation adapted by its small height and narrow leaves.

The species *Dendrosenecio meruensis*, an endemic species of Mt. Meru, is normally found within this altitude belt, but I did not find it in any of my study plots.

Montane forest composition varies considerably with rainfall and can be quite different on different sides of the same mountain at the same altitude (Hedberg 1951). Hedberg (1951) classified montane forest zone into three belts: montane rain forest belt, bamboo zone and *Hagenia-Hypericum* zone. In my results I did not find bamboo zone on the eastern slopes, This is also in accordance with the observation of Hedberg (1951), who found no distinct zone of montane rain forest and bamboo zone between 1700 and 2700 m.a.s.l on the eastern slope, although the bamboo zone is present on the southern slope. The absence of a bamboo zone in the eastern slope but presence of the southern slope can be explained by differences in rainfall at the same altitude at different sides of the mountain (Hedberg 1951).

#### **4.1.3 *Erica arborea* shrubland community.**

This community was highly dominated by *Erica arborea*, an evergreen indigenous multi-stemmed shrub with a typical height between 1 and 4 m and needle like leaves in whorls of 3 or 4 (Wesche, Miehe & Kaeppli 2000). My results show that the community occupied two altitudes, the mid altitude at 2600 m, and in the ericaceous zone at the highest altitude (3400 m). This may be explained by previous forest fires in the area.

*Erica arborea* is generally considered to be a pyrophyte (Mutch 1970; Valbuena & Vera 2002), a fire dependent species. This species can tolerate heat to 120°C, demonstrating that its seedbank survives after fire (Mutch 1970). Despite this, observations from Mesléard and Lepart (1991) showed that the species' germination is not influenced by fire. Inability of this

---

species to reseed after forest fire suggests that the relatively high temperature tolerance of seeds is not necessary an adaptation to fire (Mesléard & Lepart 1991). Light is a requirement for seed germination and survival (Mesléard & Lepart 1991). However fires favour their survival by preventing establishment of other woody species and opening up sites for germination (Mesléard & Lepart 1991; Valbuena & Vera 2002).

The seed of *Erica arborea* weighs  $1.3 \times 10^{-3}$  kg, and lacks aerial dispersal structures. Therefore, it can be carried by wind only a short distances (Mesléard & Lepart 1991). Due to its low weight, the seed is mostly dispersed by birds (Mesléard & Lepart 1991). I therefore suggest that occurrence of *Erica arborea* in open patches at the mid altitude (2600 m) was probably influenced by forest fires which opened space for seedling of *Erica arborea* and birds could be the ones who dispersed the seed through droppings.

The occurrence of the ericaceous community in different altitudes is inconsistent with Hedberg (1951), who observed the community only in higher altitude between 3100 and 3600 m. This significant upward shift of the community from 3100 to 3400 m.a.s.l could be the result of climate change. The ericaceous zone appears in different altitudes between different East African mountains, due to difference in climatic factors, edaphic divergences and forest fires caused by man (Hedberg 1951). E.g. in Mt. Elgon the ericaceous zone was found between 3200 and 3550 m, in Mt. Kenya between 3400 and 3600 m (Hedberg 1951) and between 3250 and 4000 m in Mt. Kilimanjaro (Hemp 2002).

Other species I observed in this community include *Erica excelsa* and *Hypericum revolutum*, also observed by Hedberg (1951). Hedberg (1951) called the species *Philippia excelsa* and *Hypericum leucoptychodes* but currently they have been renamed to *Erica excelsa* and *Hypericum revolutum* respectively (Dharani 2002). I also found *Agauria satcifolia* and *Stoebe kilimandscharica* in this community, which were not mentioned by Hedberg (1951).

This community had low species richness and diversity compared to the other two communities. That few species are adapted to high altitude, can probably be explained by edaphic monotony and stressful climate with high temperatures during the day and about freezing temperatures at night.

---

## 4.2 Species richness and diversity

My results showed that both species richness and diversity decreased with increasing altitude. This might be explained by reduced precipitation, atmospheric pressure, soil quality and productivity with altitude (Rahbek 1995). Barry (2008) stated that for tropical mountains, precipitation above the cloud zone decreases with altitude. Since I started my transects at 1600 m (within the cloud zone, between 1200 and 2500 m) characterized by high precipitation (Stadtmüller 1987), It is probably one of the reasons I found decreased species richness and diversity with increasing altitude. This is because few species are adapted to high altitude dry areas (Körner 2004).

Atmospheric pressure decreases by approximately 1.1% for every 100 m gain in altitude (Körner 2007), slightly varying with temperature and humidity. The decrease in atmospheric pressure has a significant effect on gas exchange in plants. Oxygen and carbon dioxide partial pressure is approximately 21% lower at 2,000 m.a.s.l than at sea level. This will therefore reduce the rate at which carbon dioxide diffuses in the leaf (Arp 1991). For this reason, species richness and diversity may decrease with altitude as few species are adapted to low partial pressure of respiratory gases.

Decreased temperature, humidity and precipitation with altitude, will affect soil nutrient concentration and soil pH (Saeed *et al.* 2014). In turn, this will decrease soil productivity along altitudinal gradients resulting in high productivity at low altitudes and decreased productivity with increasing altitude. Decreased productivity with increasing altitude results in higher species richness and diversity of plants at low compared to high altitudes (Körner 2000).

Tanner, Vitousek and Cuevas (1998) reported that soil nitrogen and phosphorus concentrations decrease with altitude and can lead to reduced plant species richness at high altitudes compared to low altitudes. During field surveys in the study area, I observed fairly coarse texture of the soil with a high percentage of sand and less fine material at high altitudes of above 3,000 m and much fine textured soil with high humus accumulation at low altitudes around 1,600 to 2,400 m.a.s.l. These observations are similar to the observations of soil texture in Lundgren and Lundgren (1972). Soil texture could also explain the high species richness and diversity at low altitudes compared with at high altitudes. Humus is

very essential in soil as it increases water holding capacity (Senn & Kingman 1973). Therefore, soil at lower altitudes with high humus accumulation has high water holding capacity and this decreases with increasing altitude. Soils with high humus accumulation may therefore support high species richness and diversity at low altitude since plants require nutrients and moisture to survive (Huston 1980). Humus decreases with decreases in moisture and temperatures along altitudinal gradients (Hedberg 1964). In addition, at low altitudes of East African mountain forests have a high biodiversity of soil microorganisms and earthworms which are essential for soil formation (Körner 2004). Diversity of soil microorganisms and earthworms decreased with altitude (Körner 2004). Therefore, low diversity of earthworms and soil-microbes and shallow soil may also contribute to low species richness and diversity of plants at higher altitudes.

The eastern slope of Mt. Meru falls within Arusha National Park. Due to strong rules and regulations of the park, there is no human impact on vegetation through deforestation, agriculture or settlements. Hence, the area sustains a high species diversity and richness in low altitudes of the mountain. This is quite different from other East African mountains such as Mt. Kilimanjaro where the hump shaped species distribution is probably influenced by human impact at the low altitude of the mountain where population is increasing from day to day, and demand of land for agriculture and settlement is increasing (Soini 2005).

It is believed that a decrease in species richness with altitude in terrestrial environments is a phenomenon which is almost as widespread as a decrease with latitude (Michael, Townsend & Harper 1990). Therefore altitudinal and latitudinal species richness gradients mirror each other (Stevens 1992). However, they differ in climate due to the day climate with altitude (Hedberg 1951) and seasonal with latitude. A decrease in species richness and diversity with altitude fits well with the general acceptance that lowland tropical rainforest has the richest biota on earth (Erwin 1988).

### 4.3 Tree height variation with altitude

I found that tree height decreased with altitude, which is consistent with the findings of Moser (2008) in South Ecuador and Lieberman *et al.* (1996) in Costa Rica. Among the possible causes for this decline is a combination of solar radiation, temperature, soil quality,

wind speed, and precipitation. Solar radiation is essential for plant survival through photosynthesis (Gómez *et al.* 1998), and it increases with altitude (Barry 2008). Trees at low altitude where density is high, grow tall as an adaptation to light competition with neighboring trees (Givnish 1988). Trees at high altitude, where competition for light is not a problem, are shorter (Givnish 1988).

Wind speed together with soil quality also affect tree height. Strong winds cause swaying of trees and striding of their roots. This movement will disturb root-soil contact, lessening water absorption and increasing of water stress (Nicoll & Ray 1996). Since wind speed increases with altitude, at high altitude where it is windy, trees are adapted to be shorter, otherwise they may break or fall over from wind. Nicoll and Ray (1996) explained how a low tree reduces the risk of the breakage in high wind.

At low altitude soil is deep which enhances anchoring of tall trees compared to the higher altitude with shallow soil (Clark, Palmer & Clark 1999). During field data collection; I did not observe plant species with buttress or prop roots in the low altitude of the study area. These structures provide mechanical support particularly for large trees on shallow soil. This suggests that the soil was deep in the low altitude of the study area than in the high. Temperature, atmospheric pressure and precipitation affect soil formation processes (weathering) (Jenny 1994), and the weathering process is high when these factors are high (Jenny 1994). Thus, at low altitudes with high temperatures, atmospheric pressures and precipitation, we expect more intense weathering processes which result in deep soil that can support taller trees. However, at high altitude with low temperatures, atmospheric pressures and precipitation we expect shallow soil which supports short trees. Height of the tree is related to upward water transport (Medina 1983). Therefore, at high altitudes, trees may also adapt to be short due to lack of enough water in the shallow soil (Medina 1983).

Decreases in air pressure with altitude decreases partial pressure of carbon dioxide (Arp 1991), which may reduce growth rate of vascular plant species at high altitudes (Hedberg 1964). A combination of these factors may result in low tree height at high altitudes compared with equivalent aged tree species in the low altitudes.

---

## 4.4 Canopy cover variation with altitude

Canopy cover refers to the vertical projection of the tree crown that covers the ground (Jennings, Brown & Sheil 1999). Canopy cover is important ecologically since it provides microclimate for other living organisms in the ecosystems. My results showed that tree canopy cover decreased with increasing altitude. This is consistent with the findings of Girardin *et al.* (2014) in Bolivia, Peru and Ecuador. Among the possible causes for this decrease is solar radiation. Solar radiation increases with increasing altitude. Tree crown projections can be related to solar radiation, as discussed for tree height. At lower altitudes trees often develop large round crowns so they can capture as much solar radiation as possible for photosynthesis (Gómez *et al.* 1998). Tree species found in high altitudes, such as, *Hypericum revolutum*, *Erica arborea* and *Stoebe kilimandscharica* have reduced canopy cover and leaf size compared to lower altitude plant species such as *Bersama abyssinica*, *Croton macrostachyus*, *Rauvolfia caffra* and others. This could probably be an adaptation to reduce severe water loss through evapotranspiration, since solar radiation increases with altitude.

Another possible cause for the reduced canopy cover with altitude is wind speed. Wind increases with altitude, this might cause canopy damage, tree falling or breaking as described with regards to tree height. At high altitude, where wind speed is high, trees may adapt by reducing their canopy, as well as their height. Due to strong winds at high altitudes, trees possess steeple - shaped crowns as an adaptation to reduce the canopy cover area hence, reduces air drag by the canopy (Ennos 1997). Species of *Hypericum revolutum*, *Erica arborea* and *Stoebe kilimandscharica*, which are found in high altitudes of Mt. Meru have steeple-shaped crowns as an adaptation to strong winds and possibly insolation along the slopes. In addition, wind speed increases the rate of transpiration by removing the moisture-laden air from around stomata openings and replacing it with dryer air (McNaughton & Jarvis 1983). The influence of wind on transpiration is high when humidity is low and soil moisture is adequate (McNaughton & Jarvis 1983). At high altitudes where it is windy, and thus, canopy cover may become lower to reduce the transpiration rate since the area has shallower soil and water availability is low.

## 4.5 Management Implications

Arusha National Park is designed to protect natural resources. The focus is mainly on protection of wildlife populations rather than plant communities. This study describes plant community distribution in Mt. Meru and shows how species richness and diversity vary with altitude. My findings have shown how altitude and associated environmental parameters can influence species distribution, diversity, richness, tree height and canopy cover I have also documented the presence of many species indigenous to Eastern Africa and one endemic species of the area (*Dendrosenecio meruensis*), which highlights that Arusha National Park also has an important function for the protection of plants, not only wildlife. This knowledge may facilitate conservation of plant communities in the future.

Since there is no study of the kind conducted in the area since Hedberg (1951), our findings could be used as baseline information for future studies particularly those aiming at studying the effect of global warming on range shifts of woody plant species. Also, this study is useful in developing an understanding of the global distribution and diversity patterns of plants since the effect of altitude on species diversity and richness mirrors that of latitudes.

As this area (Mount Meru) is not well known and has not been well studied, I therefore recommend increased focus on the conservation and management of the identified plant communities, and invite more researchers to conduct studies in the area.

## 4.6 Conclusion

This study has demonstrably shown how increasing altitude and associated environmental parameters can lead to reduced species richness, diversity, tree height and canopy cover on a tropical mountain in East Africa. This study also confirms the occurrence of three woody plant communities on Mt. Meru at different altitudes. This corresponds to three altitudinal vegetation zones as suggested by previous researchers such as Hedberg (1951) and not a continuum model as proposed by Hamilton (1975). However minor changes in vegetation composition are reported compared to Hedberg (1951), and may be the result effect of climate change or natural processes which have occurred.

## 5. ACKNOWLEDGEMENTS

I wish to express heartfelt gratitude to Ass. Prof Karen Marie Mathisen and Prof Christina Skarpe of the Faculty of Applied Ecology and Agricultural Sciences, Inland Norway University of Applied Science (INN) who tirelessly supervised this study and constantly guided me. I am particularly grateful for their valuable and constructive understanding during the course of this study. I feel proud to have had the opportunity to work under them.

I would like also to extend my gratitude to Quota scholarship programme for developing countries through Norwegian government for providing me with financial support to accomplish this programme. I am particularly indebted to College of African Wildlife Management - Mweka (CAWM) for granting me the study leave to join the programme.

I would like also to thank Tanzania Wildlife Research Institute (TAWIRI), Tanzania National Park Authority (TANAPA), and Tanzania Commission for Science and Technology (COSTECH) for giving me permission to conduct my field research in Arusha National Park (ANAPA). Without forget Mr. Emmanuel Isack Mboya from National Herbarium of Tanzania (NHT) for his superb help in plant identification during the entire period of the data collection.

My special thanks goes to my lovely wife, Flora Yessaya Pallangyo for her superb lovely care and tender encouragement during my stay at INN. Finally, to the Almighty God who give me the gift of life, health and who has made everything possible for this work to be accomplished.

Therefore, this dissertation is dedicated to my lovely kids; Neriah, Neritha and Nerius who missed me always during my absence at home and it was reaching a time where they were about to call me uncle instead of daddy.



## 6. REFERENCE

- Arp, W. (1991) Effects of source-sink relations on photosynthetic acclimation to elevated CO<sub>2</sub>. *Plant, Cell & Environment*, **14**, 869-875.
- Barry (2008) *Mountain Weather and Climate*. –Cambridge University Press. *New York*.
- Barry, R.G. (1992) *Mountain weather and climate*. Psychology Press.
- Bianchini, E., Pimenta, J.A. & dos Santos, F.A. (2001) Spatial and temporal variation in the canopy cover in a tropical semi-deciduous forest. *Brazilian Archives of Biology and Technology*, **44**, 269-276.
- Bussmann, R.W. (2006) Vegetation zonation and nomenclature of African mountains—an overview. *Lyonia*, **11**, 41-66.
- Cahill, A.E., Aiello-Lammens, M.E., Fisher-Reid, M.C., Hua, X., Karanewsky, C.J., Ryu, H.Y., Sbeglia, G.C., Spagnolo, F., Waldron, J.B. & Warsi, O. (2012) How does climate change cause extinction? *Proc. R. Soc. B*, pp. rspb20121890. The Royal Society.
- Chapman, J.D. & White, F. (1970) The evergreen forest of Malawi. *The evergreen forest of Malawi*.
- Clark, D.B., Palmer, M.W. & Clark, D.A. (1999) Edaphic factors and the landscape-scale distributions of tropical rain forest trees. *Ecology*, **80**, 2662-2675.
- Coetzee, J. (1978) Phytogeographical aspects of the montane forests of the chain of mountains on the eastern side of Africa. *Erdwiss. Forsch. Akad. Wiss. Lit.(Germany)*, **11**, 482-494.
- Coomes, D.A. & Allen, R.B. (2007) Effects of size, competition and altitude on tree growth. *Journal of Ecology*, **95**, 1084-1097.
- Crawley, M.J. (2007) *The R book*. Hoboken. NJ: Wiley.
- d'Arge, R., Limburg, K., Grasso, M., de Groot, R., Faber, S., O'Neill, R., Van den Belt, M., Paruelo, J., Raskin, R. & Costanza, R. (1997) The value of the world's ecosystem services and natural capital.
- Dharani, N. (2002) *Field guide to common trees & shrubs of East Africa*. Struik.
- Ennos, A. (1997) Wind as an ecological factor. *Trends in ecology & evolution*, **12**, 108-111.
- Erwin, T.L. (1988) The tropical forest canopy. *Biodiversity*, 123-129.
- Gauch, H.G. (1982) *Multivariate analysis in community ecology*. Cambridge University Press.
- Girardin, C.A., Farfan-Rios, W., Garcia, K., Feeley, K.J., Jørgensen, P.M., Murakami, A.A., Cayola Pérez, L., Seidel, R., Paniagua, N. & Fuentes Claros, A.F. (2014) Spatial patterns of above-ground structure, biomass and composition in a network of six Andean elevation transects. *Plant Ecology & Diversity*, **7**, 161-171.

- 
- Givnish, T.J. (1988) Adaptation to sun and shade: a whole-plant perspective. *Functional Plant Biology*, **15**, 63-92.
- Gómez, I., Pérez-Rodríguez, E., Viñepla, B., Figueroa, F.L. & Karsten, U. (1998) Effects of solar radiation on photosynthesis, UV-absorbing compounds and enzyme activities of the green alga *Dasycladus vermicularis* from southern Spain. *Journal of Photochemistry and Photobiology B: Biology*, **47**, 46-57.
- Grytnes, J.A. (2003) Species-richness patterns of vascular plants along seven altitudinal transects in Norway. *Ecography*, **26**, 291-300.
- Grytnes, J.A. & Beaman, J.H. (2006) Elevational species richness patterns for vascular plants on Mount Kinabalu, Borneo. *Journal of Biogeography*, **33**, 1838-1849.
- Guo, Q., Kelt, D.A., Sun, Z., Liu, H., Hu, L., Ren, H. & Wen, J. (2013) Global variation in elevational diversity patterns. *Scientific reports*, **3**.
- Hamilton, A. (1975) A quantitative analysis of altitudinal zonation in Uganda forests. *Plant Ecology*, **30**, 99-106.
- Hamilton, A.C. (1982) *Environmental history of East Africa: a study of the Quaternary*. Academic press London.
- Hedberg, I. & Hedberg, O. (1979) Tropical-alpine life-forms of vascular plants. *Oikos*, 297-307.
- Hedberg, O. (1951) Vegetation belts of the East African mountains. *Svensk Bot. Tidsk*, **45**, 140-202.
- Hedberg, O. (1964) *Afroalpine plant ecology*. Almqvist & Wiksell.
- Hemp, A. (2002) Ecology of the pteridophytes on the southern slopes of Mt. Kilimanjaro—I. Altitudinal distribution. *Plant Ecology*, **159**, 211-239.
- Hemp, A. (2006a) Continuum or zonation? Altitudinal gradients in the forest vegetation of Mt. Kilimanjaro. *Plant Ecology*, **184**, 27-42.
- Hemp, A. (2006b) Vegetation of Kilimanjaro: hidden endemics and missing bamboo. *African Journal of Ecology*, **44**, 305-328.
- Hunter, M.L. & Yonzon, P. (1993) Altitudinal distributions of birds, mammals, people, forests, and parks in Nepal. *Conservation Biology*, 420-423.
- Huston, M. (1980) Soil nutrients and tree species richness in Costa Rican forests. *Journal of Biogeography*, 147-157.
- Jennings, S., Brown, N. & Sheil, D. (1999) Assessing forest canopies and understorey illumination: canopy closure, canopy cover and other measures. *Forestry*, **72**, 59-74.
- Jenny, H. (1994) *Factors of soil formation: a system of quantitative pedology*. Courier Corporation.
- Kahana, L.W., Malan, G. & Sylvina, T.J. (2015) Glade use by Olive baboons and Blue monkeys in Mount Meru Game Reserve, Tanzania. *African Journal of Ecology*, **53**, 362-374.

- 
- Kelly, A.E. & Goulden, M.L. (2008) Rapid shifts in plant distribution with recent climate change. *Proceedings of the National Academy of Sciences*, **105**, 11823-11826.
- Kitayama, K. & Aiba, S.I. (2002) Ecosystem structure and productivity of tropical rain forests along altitudinal gradients with contrasting soil phosphorus pools on Mount Kinabalu, Borneo. *Journal of Ecology*, **90**, 37-51.
- Körner, C. (2000) Why are there global gradients in species richness? Mountains might hold the answer. *Trends in ecology & evolution*, **15**, 513-514.
- Körner, C. (2004) Mountain biodiversity, its causes and function. *Ambio*, 11-17.
- Körner, C. (2007) The use of 'altitude' in ecological research. *Trends in ecology & evolution*, **22**, 569-574.
- Krebs, C.J. (1989) *Ecological methodology*. Harper & Row New York.
- La Mantia, T., Giaini, G., Veca, D.S.L.M. & Pasta, S. (2007) The role of traditional Erica arborea L. management practices in maintaining northeastern Sicily's cultural landscape. *Forest ecology and management*, **249**, 63-70.
- Lawson, D.W., Mulder, M.B., Ghiselli, M.E., Ngadaya, E., Ngowi, B., Mfinanga, S.G., Hartwig, K. & James, S. (2014) Ethnicity and child health in northern Tanzania: Maasai pastoralists are disadvantaged compared to neighbouring ethnic groups. *PLoS One*, **9**, e110447.
- Lawton, R.O. (1982) Wind stress and elfin stature in a montane rain forest tree: an adaptive explanation. *American Journal of Botany*, 1224-1230.
- Lenoir, J., Gégout, J.-C., Marquet, P., De Ruffray, P. & Brisse, H. (2008) A significant upward shift in plant species optimum elevation during the 20th century. *science*, **320**, 1768-1771.
- Lieberman, D., Lieberman, M., Peralta, R. & Hartshorn, G.S. (1996) Tropical forest structure and composition on a large-scale altitudinal gradient in Costa Rica. *Journal of Ecology*, 137-152.
- Lundgren, B. & Lundgren, L. (1972) Comparison of some soil properties in one forest and two grassland ecosystems on Mount Meru, Tanzania. *Geografiska Annaler. Series A. Physical Geography*, 227-240.
- Magurran, A.E. (2013) *Measuring biological diversity*. John Wiley & Sons.
- Mangubuli, J. & Lyamuya, V. (1988) A survey of habitat in Mount Meru Forest Game Reserve Tanzania. Technical Report, College of African Wildlife Management Mweka.
- McCain, C.M. (2010) Elevational gradients in species richness. *eLS*.
- McCain, C.M. & Grytnes, J.A. (2010) Elevational gradients in species richness. *eLS*.
- McCullagh, P. & Nelder, J.A. (1989) *Generalized linear models*. CRC press.
- McNaughton, K. & Jarvis, P. (1983) Predicting effects of vegetation changes on transpiration and evaporation. *Water deficits and plant growth*, **7**, 1-47.

- 
- Medina, E. (1983) Adaptations of tropical trees to moisture stress. *Ecosystems of the world: tropical rain forest ecosystems*. Amsterdam: Elsevier Scientific Publishing Co, 225-237.
- Mesléard, F. & Lepart, J. (1991) Germination and seedling dynamics of *Arbutus unedo* and *Erica arborea* on Corsica. *Journal of Vegetation Science*, **2**, 155-164.
- Michael, B., Townsend, C. & Harper, J. (1990) *Ecology: Individuals, Populations and Communities*. BlackwellScienceInc.
- Moser, G. (2008) Altitudinal changes in stand structure and biomass allocation of tropical mountain forests in relation to microclimate and soil chemistry. *Gradients in a tropical mountain ecosystem of Ecuador*, pp. 229-242. Springer.
- Mutch, R.W. (1970) Wildland Fires and Ecosystems--A Hypothesis. *Ecology*, **51**, 1046-1051.
- Nicoll, B.C. & Ray, D. (1996) Adaptive growth of tree root systems in response to wind action and site conditions. *Tree physiology*, **16**, 891-898.
- Niemelä, T. & Pellikka, P. (2004) Zonation and characteristics of the vegetation of Mt. Kenya. *Taita Hills and Kenya*, 14-20.
- Odland, A. & Birks, H. (1999) The altitudinal gradient of vascular plant richness in Aurland, western Norway. *Ecography*, **22**, 548-566.
- Pedroni, F., Eisenlohr, P.V. & Oliveira-Filho, A.T. (2013) Changes in tree community composition and structure of Atlantic rain forest on a slope of the Serra do Mar range, southeastern Brazil, from near sea level to 1000m of altitude. *Flora-Morphology, Distribution, Functional Ecology of Plants*, **208**, 184-196.
- Rahbek, C. (1995) The elevational gradient of species richness: a uniform pattern? *Ecography*, **18**, 200-205.
- Razzetti, E. & Msuya, C.A. (2002) *Field guide to the amphibians and reptiles of Arusha National Park (Tanzania)*. TANAPA.
- Saeed, S., Barozai, M.Y.K., Ahmad, A. & Shah, S.H. (2014) Impact of altitude on soil physical and chemical properties in Sra Ghurgai (Takatu mountain range) Quetta, Balochistan. *International Journal of Scientific and Engineering Research*, **5**, 730-735.
- Sarmiento, G. (1986) Ecological features of climate in high tropical mountains. *High altitude tropical biogeography*, 11-45.
- Senn, T. & Kingman, A.R. (1973) A review of humus and humic acids. *Research Series Report*.
- Šmilauer, P. & Lepš, J. (2014) *Multivariate analysis of ecological data using CANOCO 5*. Cambridge university press.
- Soini, E. (2005) Land use change patterns and livelihood dynamics on the slopes of Mt. Kilimanjaro, Tanzania. *Agricultural Systems*, **85**, 306-323.

- Stadtmüller, T. (1987) *Cloud forests in the humid tropics: a bibliographic review*. Bib. Orton IICA/CATIE.
- Stevens, G.C. (1992) The elevational gradient in altitudinal range: an extension of Rapoport's latitudinal rule to altitude. *The American Naturalist*, **140**, 893-911.
- TANAPA (2017) *Tanzania National Park*. (Accessed 26 April, 2017). <http://www.tanzaniaparks.go.tz/>
- Tanner, E., Vitousek, P. & Cuevas, E. (1998) Experimental investigation of nutrient limitation of forest growth on wet tropical mountains. *Ecology*, **79**, 10-22.
- Turrill, W.B. & Milne-Redhead, E. (1952) Flora of tropical East Africa. *Flora of Tropical East Africa*.
- Valbuena, L. & Vera, M. (2002) The effects of thermal scarification and seed storage on germination of four heathland species. *Plant Ecology*, **161**, 137-144.
- Wesche, K., Miehe, G. & Kaeppeli, M. (2000) The significance of fire for afroalpine ericaceous vegetation. *Mountain Research and Development*, **20**, 340-347.