

Species richness, vegetation structure, and floristic composition of woody plants along the elevation gradient of Mt. Meru, Tanzania

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Abstract

Understanding the change in vegetation composition along elevational gradients is critical for species conservation in a changing world. We studied the species richness, tree height, and floristic composition of woody plants along an elevation gradient of protected habitats on the eastern slope of Mount Meru and analyzed how these vegetation variables are influenced by the interplay of temperature and precipitation. Vegetation data were collected on 44 plots systematically placed along five transects spanning an elevational gradient of 1600 to 3400 m a.s.l. We used ordinary linear models and multivariate analyses to test the effect of mean annual temperature and precipitation on woody plant species richness, tree height, and floristic composition. We found that species richness, mean tree height, and maximum tree height declined monotonically with elevation. Models that included only mean annual temperature as an explanatory variable were generally best supported to predict changes in species richness and tree height along the elevation gradient. We found significant changes in woody plant floristic composition with elevation, which were shaped by an interaction of mean annual temperature and precipitation. While plant communities consistently changed with temperature along the elevation gradient, levels of precipitation were more important for plant communities at lower than for those at higher elevations. Our study suggests that changes in temperature and precipitation regimes in the course of climate change will reshape elevational gradients of diversity, tree height, and correlated carbon storage in ecosystems, and the sequence of tree communities on East African mountains.

KEYWORDS

Arusha National Park, floristic diversity, mean annual precipitation, mean annual temperature, mountain, tree height, woody plant community

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1 | INTRODUCTION

Mountains cover about 25% of the earth's land surface, hosting at least one-third of the terrestrial plant species (Corlett, 2016; Cremeens, 2012; Körner, 2007; Rahbek et al., 2019). In mountainous areas, vegetation composition, floristic diversity, and forest structure change with elevation (Grytnes & Beaman, 2006; Guo et al., 2013; Sainge et al., 2019; Sanchez et al., 2013). These vegetation changes are related to several abiotic factors that include atmospheric pressure, solar radiation, soil quality, and in particular changes in air temperature and precipitation along the elevation gradient (Körner, 2007; McCain & Grytnes, 2010; Peters et al., 2016, 2019; Rahbek et al., 2019). Understanding how and why the structure and composition of the vegetation vary along elevational gradients is critical for developing conservation plans and predicting the impacts of global climatic change on ecosystems (Grytnes, 2003; Peters et al., 2019). Besides, knowledge about this variation will facilitate the protection and management of rare and threatened plant species, hence maintaining ecological patterns and ecosystem services (Costanza et al., 1997; Roos et al., 2019; Watkins et al., 2006).

Plants are key structural elements of the terrestrial ecosystem (Kreft & Jetz, 2007). They act as a primary producer in the ecosystem and sources of all terrestrial food webs (Kreft & Jetz, 2007; Martyniuk et al., 2016). Numbers of studies have shown a remarkably strong association between climatic variables and species richness (Lasway, Peters, et al., 2022; Lasway, Steffan-Dewenter, et al., 2022; Peters et al., 2016). As thermal niches of mountain species, particularly of tropical species, are typically small, changes in temperature with elevation are associated with strong alteration of the floristic communities (Currie et al., 2004; Peters et al., 2019; Qian et al., 2003; Zhang et al., 2009). Moreover, water and water-related variables have been found to be major predictors of global vascular plant species richness (Francis & Currie, 2003; Kreft & Jetz, 2007; Peters et al., 2016). Nevertheless, their interaction in determining woody plant species richness and vegetation composition along the elevational gradient is less reported. Therefore, this study intended to infer which abiotic factor has a strong effect on woody plant species richness, vegetation structure, and composition and whether their interaction or additive effect could have a significant impact.

We analyzed changes in the woody plant species richness, tree height, and vegetation composition along an elevational gradient of well-protected habitats in the Arusha National Park on the eastern slopes of Mt. Meru, Tanzania. The vegetation of Mt. Meru was already partly studied by Hedberg (1951) and Bussmann (2006). However, their studies focused much on delimitating vegetation belts and nomenclature. They did not relate the changes in the woody plant species richness, vegetation structure, and species composition to climate variables. Conversely, reports show that most studies conducted in the study area focused on the inventories of small mammals (Demeter & Hutterer, 1986; Stanley & Kihale, 2016), birds (Beesley, 1972; Kahana et al., 2013), and invertebrates (Lasway et al., 2021; Pauly et al., 2019; Tommasi et al., 2021).

Here we tested whether the mean annual temperature (MAT) and mean annual precipitation (MAP) could explain the changes observed in plant communities. We also tested whether the interaction between MAT and MAP is a better predictor of changes in woody plant biodiversity than MAT, MAP, or their additive effects. In case of a significant interaction, the effects of one predictor variable are depending on the size of the other, for example, implying stronger effects of precipitation at high or low temperatures or vice versa.

2 | METHODS

2.1 | Study area description

This study was conducted along the eastern slopes of Mt. Meru (ca. 36°45' E–3°15' S) within the Arusha National Park, Tanzania (Figure 1). The park covers about 552 km² (Mahenya & Chacha, 2020). In the lowland at 1600m above sea level (a.s.l.), the annual mean maximum temperature (the hottest season) is 25.4°C in January and February and the annual mean minimum temperature (the coldest season) is 12.8°C in July and August (Kahana et al., 2015). Mean annual temperature (MAT) decreases quasi-linearly with elevation, with a lapse rate of approximately 0.6°C per 100m gain in elevation, reaching ca. –2°C at the top of the mountain (Karger et al., 2017). The area has two rainy seasons: a long rainy season between ca. March and May and a short rainy season between ca. November and December. The average MAP corresponds to ca. 1300mm in the lowlands, rising to ca. 1600mm at approximately 2500m a.s.l. and then decreasing again above the cloud zone in the higher elevations (Karger et al., 2017). The soil of Mt. Meru originates from the volcanic activities of the mountain which is formed by loose and light volcanic ashes that make it susceptible to erosion in the absence of vegetation cover (Lasway et al., 2023; Lundgren, 1978).

2.2 | History of the study area

Mt. Meru is a relatively young volcanic mountain with two peaks, Mt. Meru summit (4566m a.s.l.) and Little Meru (3820m a.s.l.). The mountain was formed during the late Pleistocene time, 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. 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 Reserve and was later declared as a Game Reserve in 1946 (Lundgren & Lundgren, 1972). The area was upgraded to a National Park in 1960 and the whole Eastern side of the mountain was included in Arusha National Park (Lundgren & Lundgren, 1972), giving it a high level of

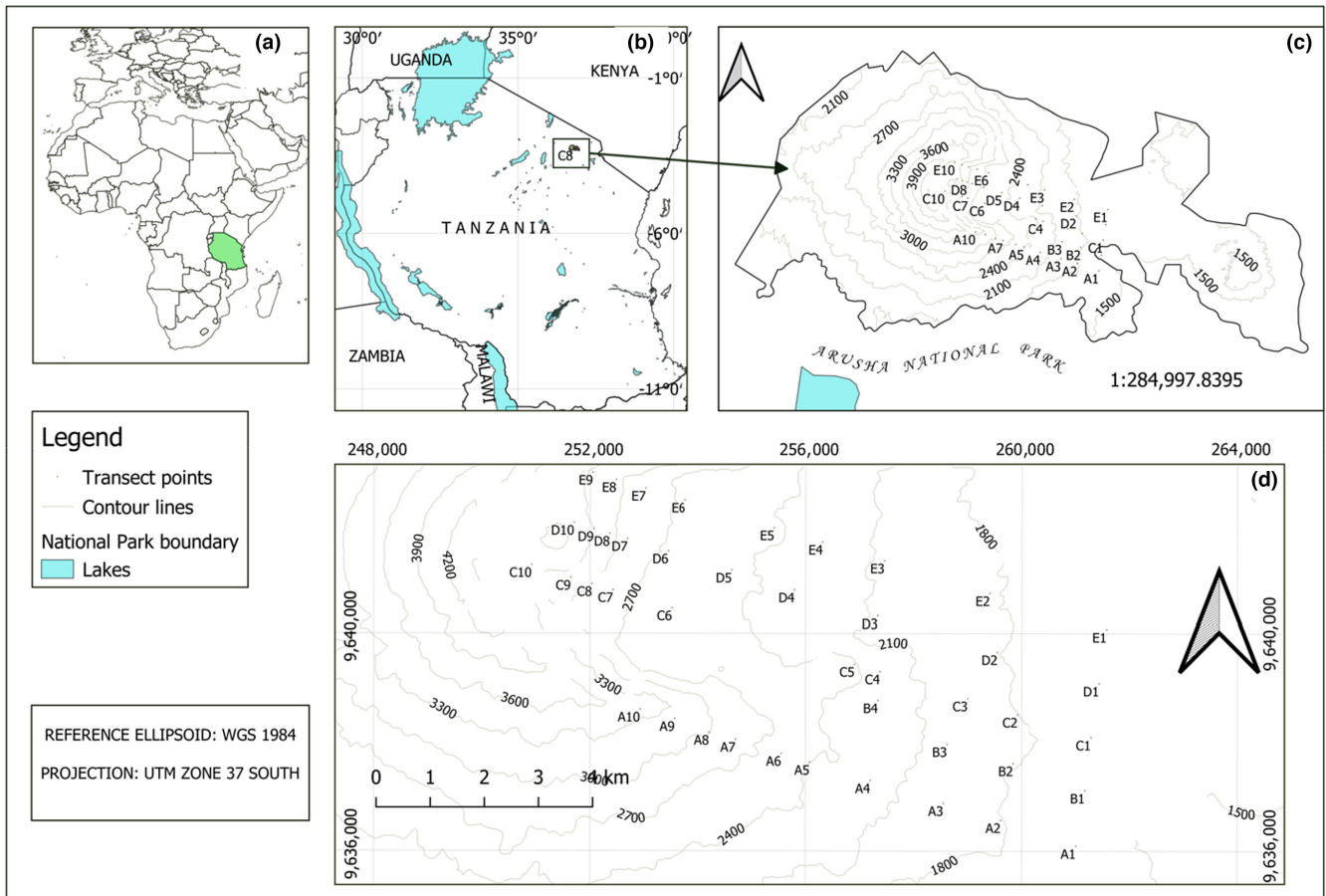


FIGURE 1 Map of Arusha National Park (c) showing the distribution of plots (indicated by combinations of letters and numbers) on transects along the eastern slopes of Mt. Meru. The location in Africa and Tanzania is shown in (a) and (b), respectively. (d) More detailed images of plot locations.

protection. The vegetation composition of Mt. Meru varies between different sides of the mountain at equivalent elevations due to the variation in the amount of precipitation received. The eastern side of the mountain is the windward side receiving moisture-laden air (Stanley & Kihauale, 2016). During the data collection, we did not see obvious signs of logging, and we cannot fully exclude the possibility that since the establishment of the National Park in the 1960s some degree of human disturbance might have affected the vegetation.

2.3 | Data collection

Data were collected from February to April 2016 by using plot-based sampling (Sutherland, 2006). Since we were interested in understanding the change in woody plant communities along the elevational gradient, we set five transects along an elevation gradient ranging from 1600m to 3400m a.s.l. on the eastern side of the mountain (Figure 1), considering a relatively long continuous slope with uniform aspect. To obviate overlapping of the transect lines, all transect were laid out along a constant bearing of 287 degrees from the first point at 1600m a.s.l. Transects and plot locations were positioned systematically using ArcGIS version 10.3, from the lowlands escalating to the

western part of the mountain while keeping within the borders of the park. The distance from one transect to another was 1km with individual plots on transects placed at increments of 200m of elevation. The 1km transect interspatial distance aimed to cover the entire eastern side of the mountain. An elevation increment of 200m was chosen because it was feasible and detailed enough to recover the major trends in biodiversity with elevation. Each study plot had a size of 10 × 10m (Sutherland, 2006) and was always positioned on the northern side of a transect along the transect line. When the plot fell on areas modified by humans as huts or viewpoints, or in the case of rivers, we set a new plot shifted 50m to the west. We planned a total of 50 plots equally distributed over the five transects, from which only 44 could be used due to logistic constraints in reaching some of the plots. While there are areas on Mt. Meru that are known to hold very tall trees, we followed a strict systematic and nonbiased way of study plot selection to derive the “typical” vegetation change with elevation on the eastern slopes of Mt. Meru.

Our choice is to include only transects on the eastern side of the mountain because it is the only side of the mountain that is confined within the boundary of Arusha National Park. This offered us the opportunity to study changes along a well-protected elevational gradient. Areas outside of the National Park are strongly degraded

and would not be adequate for inclusion in this study. Similarly, we chose to start our transect at 1600 m.a.s.l. because most land areas below 1600 m.a.s.l. is outside of the park boundary, and affected by different types of human land use.

Some parts of the Arusha National Park extended to 1400 m.a.s.l. but were not included in the study because they were distant from the remaining study plots (>10 km) and only in one small area, which could potentially cause a problem of spatial autocorrelation. Our transects were limited to a maximum elevation of 3400 m.a.s.l. because the vegetation above this area is mostly dominated by nonwoody plants such as *Festuca sp* and *Koeleria capensis* and many everlasting flowers such as *Helichrysum spp* (*H. meyer-johannis*, *H. kilimanjari*, *H. cymosum*, *H. splendidum*, *H. newii*, *H. citripium*, etc.), *Kniphofia thomsonii*, *Cyperus phleoides*, *Gladiolus watsonides*, *Artemisia afra*, and *Koeleria capensis*.

To locate each plot for observation and recording, we used a Garmin GPSMAP 64s GPS receiver (USA). In each sampling plot, we counted and identified all woody plants with at least one-meter height. Woody plant species were identified based on the nomenclature system established by Plants of the World Online | Kew Science (2023). Tree heights greater than 5 m were measured in meters using a Suunto clinometer from the ground to the top of the highest living shoot, while those less than 5 m trees were measured by a meter scale measuring pole. Elevation was measured at the center of each plot using the GPS. Mean tree height was obtained by averaging the individual height of all trees per plot, while the maximum tree height was the height of the highest tree in a plot.

Climate data of MAT and MAP were obtained from CHELSA (Climatologies at high resolution for the earth's land surface areas; Karger et al., 2017) based on the geographic coordinates of each study plot along an elevational gradient. CHELSA climate data were used because the dataset provides monthly data of precipitation and temperature of the entire globe at a very high resolution (30 arcs, ~1 km) and performs very well even in mountainous areas (Karger et al., 2017).

2.4 | Data analysis

Data were analyzed using the R statistical platform version 4.0.3 (<http://cran.r-project.org/>). We used generalized additive models (GAMs) from the R package *mgcv* (Wood, 2017) to visualize the relationship between elevation, MAT and MAP (explanatory variables) and other response variables: the total number of species per study plot (woody plant species richness), mean tree height, and maximum tree height. In GAMs, nonparametric smoothers are used to determine the relationship between response and explanatory variables allowing flexible estimations of both linear and nonlinear relationships (Wood, 2017). We used the Gaussian data family and set the smooth function to $k=5$ to prevent the overparameterization of GAM models.

In order to test the influence of climate variables on woody plant variables, we applied ordinary linear models, assuming a linear relationship between MAT and MAP and the vegetation variables.

For each response variable, we constructed five different models:

1. $y \sim \text{MAT}$
2. $y \sim \text{MAP}$
3. $y \sim \text{MAT} + \text{MAP}$ (additive effect)
4. $y \sim \text{MAT} \times \text{MAP}$ (interactive effect), and
5. $y \sim 1$ (null model)

We used the Akaike Information Criterion with a second-order bias correction (AIC_c) for selecting the model best supported by the data. For the best model, we calculated parameter estimates and the significance level of all explanatory variables.

To visualize the effect of climate on vegetation composition, nonmetric multidimensional scaling (NMDS) was applied based on a dissimilarity matrix calculated with the Jaccard index of dissimilarity (Oksanen et al., 2020). To test the significance of the effect of climate variables on species community composition, the Adonis function in the *vegan* R package library was used (Oksanen et al., 2020). The test was based on the same dissimilarity matrix used for the NMDS. The Adonis function calculates the statistical significance for the effects of explanatory variables through a permutation procedure (permutational multivariate analysis of variance; Anderson, 2011; McArdle & Anderson, 2001) with the number of permutations set to 999. We started with Adonis model testing for an interactive effect of MAT and MAP and simplified it by successively deleting nonsignificant explanatory variables from the model. In addition to the permutational multivariate analysis of variance, we also performed a model-based analysis of multivariate abundance data, as implemented in the R package *mvabund*. Here, the data family was set to negative binomial and 999 resampling interactions were used to test the significance of MAT, MAP, and their interaction.

3 | RESULTS

3.1 | Richness of woody plant and tree height

We counted a total of 559 woody plants from 35 species across the 44 study plots. Woody plant species richness, mean tree height, and maximum tree height showed a monotonic decline with elevation (Figure 2). Woody plant species richness peaked with five species per plot in the lower elevation and decreased linearly to ca. 3 species in the higher elevation (3400 m.a.s.l.; GAM, ED=28.4%, $p < .001$). Mean tree height peaked at the lowest elevation with 9 m and moderately declined to an average of 6.5 m in the cloud zone (around 2800 m.a.s.l.) before it sharply declined to 1 m height at 3400 m.a.s.l. (GAM, ED=60.7%, $p < .001$). Similarly, maximum tree height peaked in the lowest elevation with an average of ~20 m and decreased to an average of ~5 m at 3400 m.a.s.l. (GAM, ED=81.7%, $p < .001$).

Mean annual temperature linearly decreased with elevation (GAM, ED=98.2%, $p < .001$; Figure 3a), while MAP showed a unimodal distribution pattern (Figure 3b) with a peak at the cloud zone (2800 m.a.s.l.; GAM, ED=82.6%, $p < .001$). The best supported model to explain

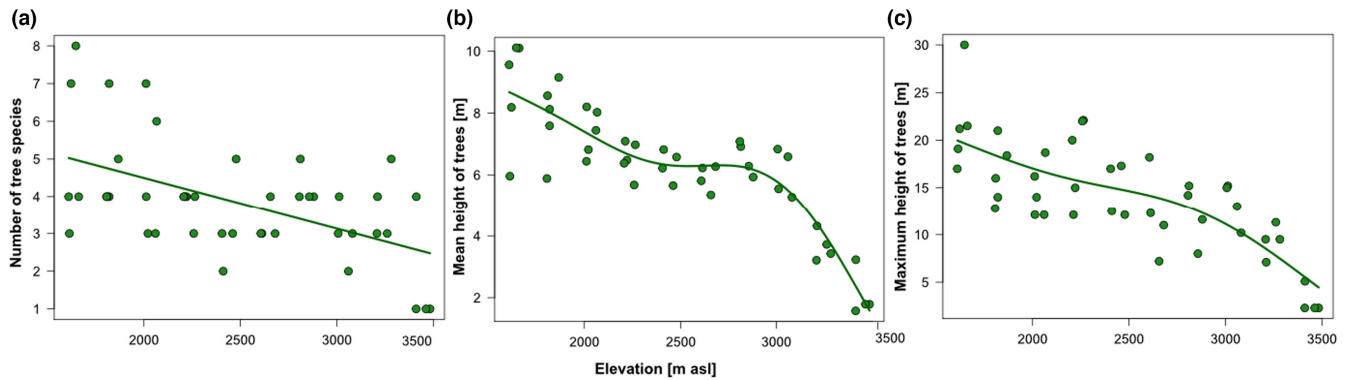


FIGURE 2 Richness of woody plants (a), mean tree height (b), and maximum tree height (c) decreased with elevation from 1600 to 3400 m a.s.l.

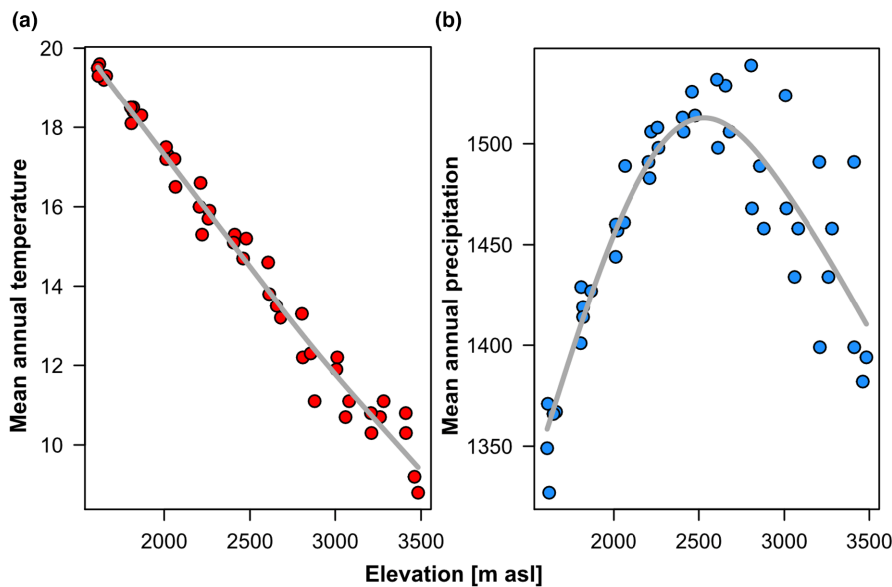


FIGURE 3 Change in mean annual temperature (a) and mean annual precipitation (b) with elevation.

the variation in woody plant species richness, maximum tree height, and mean tree height only included MAT as an explanatory variable. Models including MAP as an explanatory variable or null models were less supported by the data (Richness of woody plant, $\Delta AIC_C > 1.74$; mean tree height, $\Delta AIC_C > 1.64$; maximum tree height, $\Delta AIC_C > 1.26$). Evaluation of best models showed that woody plant species richness significantly increased with MAT ($F_{1,42} = 16.7$, $p < .001$, $R^2 = 28.5\%$) with a slope of 0.25 ± 0.06 (mean \pm SE). Similarly, mean tree height and maximum tree height significantly increased with MAT ($F_{1,42} = 77.96$, $p < .001$, $R^2 = 64.9\%$) with a slope corresponding to 0.50 ± 0.06 and 1.30 ± 0.19 ($F_{1,42} = 48.93$, $p < .001$, $R^2 = 53.8\%$), respectively.

3.2 | Species composition

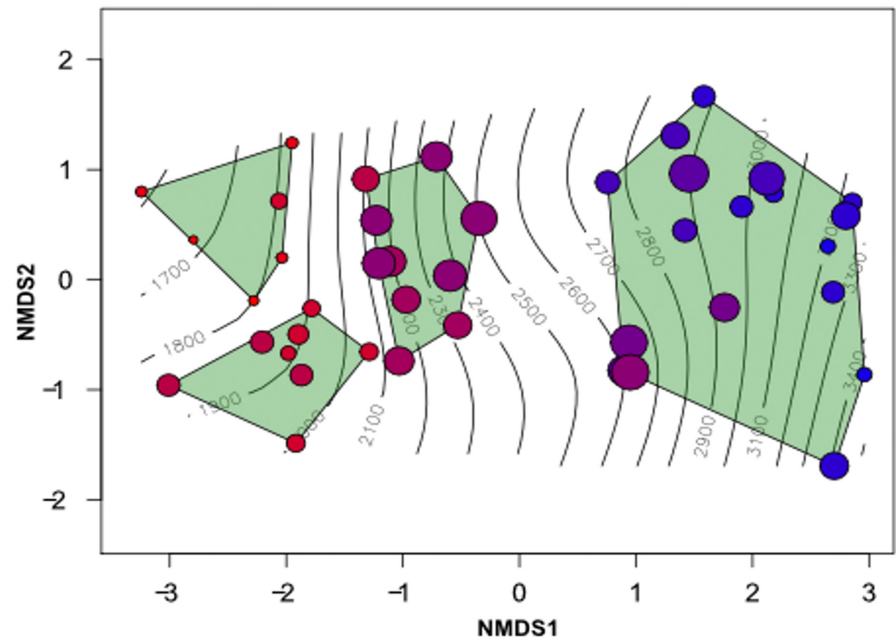
Nonmetric multidimensional scaling revealed a significant change in woody vegetation composition with elevation. Using a permutational MANOVA analysis (i.e., the Adonis function in the R package *vegan*), we found that MAT and MAP had interacting effects on the woody plant species composition (MAT: $F = 7.23$, $p = .001$, MAP:

$F = 3.50$, $p = .001$; MAT \times MAP: $F = 2.6618$, $p = .002$). A similar result was found in a model-based analysis of multivariate community data (manyglm function in the R package *mvabund*; MAT: Wald test statistic = 7.45, $p = .008$, MAP: Wald test statistic = 7.93, $p = .007$, MAT \times MAP: Wald test statistic = 7.64, $p = .007$). The interaction effect indicated that MAP had stronger effects on species communities in the arid lowland than in the cold and humid higher elevations, revealing four woody plant clusters (Figure 4): one cluster in the warm lowland with low precipitation (1600–2100 m a.s.l.), one in the lowland with higher precipitation, one in the wet and moderately warm midelevations (between 2100 and 2500 m a.s.l.), and one at the cold, higher elevation above 2800 m a.s.l.

4 | DISCUSSION

We found that woody plant species richness, mean tree height, and maximum tree height declined monotonically with elevation. The decline was best explained by changes in MAT along the elevational gradient. In contrast, we found that the species composition was

FIGURE 4 Nonmetric multidimensional scaling (NMDS) of woody plant community composition based on the Jaccard index of dissimilarity (Stress=0.07). The size of the dots represents the amount of precipitation received (small dots: low precipitation; large dots: higher precipitation), while color indicates temperature (from red=high temperature to blue=lower temperature). Green polygons indicate four clusters with distinct floristic composition referred to in the main text. Contour lines in the background indicate approximate elevational levels (increment: 100m).



depending on both MAT and MAP, with MAP having a stronger effect in the warm lowlands than in cold highland tree communities.

4.1 | The elevational pattern of woody plant species richness

The highest species richness of woody plants was recorded at the lowest studied elevations (1600 m.a.s.l.) with about five species of trees per 10x10m plot. The number of tree species decreased monotonically to about three species at a higher elevation (~3400 m.a.s.l.). The monotonous decline in species richness is similar to that found by Berhanu et al. (2017) in the Afromontane vegetation of Ethiopia and Peters et al. (2016) on plants on Mt. Kilimanjaro. The majority of elevation studies on plant species richness report a decrease in species richness with increasing elevation (Berhanu et al., 2017; Cirimwami et al., 2019; Imani et al., 2016; Peters et al., 2016; Sainge et al., 2019). However, hump-shaped patterns (peaking at mid-elevation) of species richness have also been observed (Aynekulu et al., 2012; Kitayama, 1992; Tu et al., 2010). An important aspect, which is often related to the elevational-richness pattern, is the spatial scale of the studied elevational gradient (Nogués-Bravo et al., 2008). Hump-shaped patterns are more often found when complete elevation gradients (starting at approximately sea level) are studied, while on mountains lacking the lowest elevations or on mountains where the lowlands have already been degraded by human impact more often linear-decline patterns are detected. At Mt. Meru, our lowest study site was located at 1600 m.a.s.l. It could be possible that an extension of the study to the lower and drier elevations would reveal a hump-shaped species richness pattern for woody plants. Unfortunately, lower areas in the nearness of other study plots could not be included as these areas are outside of the

Arusha National Park and largely degraded by human impact, which would have made it impossible to disentangle climatic effects from those of human land use (Peters et al., 2019).

Nevertheless, our findings based on a shorter elevation gradient than a study on the nearby Mt. Kilimanjaro Peters et al. (2016) come to the same conclusion concerning the major drivers of plant species richness: that MAT more so than MAP is the main predictor of species richness. This finding is in line with the temperature-richness hypothesis, assuming a higher evolutionary tempo and higher diversification rates in warmer environments (Brown, 2014; Rohde, 1992). Alternatively, it could be explained by higher relevance of negative-density-dependent effects in warmer environments (LaManna et al., 2017). A study by Moser et al. (2008) and Kostenko (2017) revealed that mineralization rate and the availability of soil nitrogen (and likely of other nutrients) decrease with elevation in tropical montane forests. If soil nitrogen is closely connected to species richness in plant communities (Shirima et al., 2015), this could also explain the observed decrease in woody plant species richness at higher elevations. Furthermore, lack of stable and conducive environmental conditions at higher elevations could be a reason for the low species richness (Xu et al., 2017). For instance, low temperatures at a higher elevation are associated with a decrease in humidity that in turn affects plant physiology, soil nutrient concentration, and soil pH (Saeed et al., 2014).

Unexpectedly, we did not find an effect of MAP on woody plant species richness of trees. In global studies of plant communities, both MAP and MAT were found to be important predictor variables of species richness (Kreft & Jetz, 2007). The lack of an effect of MAP on species richness observed in our study could be due to the restricted elevational range and hence range in precipitation. The lowest elevation has already rather high precipitation (at 1600 m.a.s.l.) and generally rather high amounts of rain at all elevations. Probably, within the studied environmental amplitude, rainfall was not a

limiting factor for primary productivity, the survival of species populations, and the coexistence of species.

4.2 | The elevational pattern of tree height

Both mean tree height and maximum tree height showed a monotonic decrease with elevation. At the lower elevation, mean tree height peak at 9 m and moderately decreased to an average of 6.5 m in the cloud zone (around 2800 m a.s.l.) to sharply decline to 1 m height at 3400 m a.s.l. Similarly, maximum tree height peaked in the lowest elevation with an average of ~20 m and decreased to an average of ~5 m. This decline in maximum tree height with elevation is consistent with the findings reported by Moser et al. (2008) and Lieberman et al. (1996) in southern Ecuador and Costa Rica, respectively. A monotonic decline in the mean tree height with elevation has already been reported by Wang et al. (2012) in Sygera Mountains of Southeastern Tibetan Plateau in China. On Mt. Kilimanjaro, Rutten et al. (2015) revealed a hump-shaped pattern in tree height. A major difference between our finding and those of the nearby Mt. Kilimanjaro was that the elevational gradient studied at Mt. Kilimanjaro included lowland dry savannah areas which had significantly smaller trees than highland montane forests.

We found that the MAT but not MAP was an influential predictor of mean tree height and maximum tree height along the elevation gradient. Probably, this is because of the low temperature at higher elevations that induces water stress (Mayr, 2007) that limits tree height by affecting key aspects of tree performance (Wang et al., 2012). On the flip side, low temperature at the higher elevations restricts physiological processes responsible for tissue formation such as photosynthesis and shoot growth (Koch et al., 2004; Wang et al., 2012), which results in short tree heights at the higher elevations. The decrease in tree height at higher elevations could also be explained by the low precipitation availability (Smith & Beaulieu, 2009). At higher elevations, short-height trees need less water to construct pulps and transport nutrients unlike tall trees at the lower elevations (Smith & Beaulieu, 2009).

As pointed out already in a previous section, precipitation showed a weak and rarely significant effect with tree height. Probably, this is because of the short elevation gradient of our study.

Another environmental variable that could explain short trees at the higher elevations is wind speed and fire. Wind speed is higher at higher elevations (Körner, 2007). This may lead to the swaying of trees, breaking off stems, and striding their roots (Thomas et al., 2015), a situation that disturbs root-soil contact, lessening water absorption, and increasing water stress (Nicoll & Ray, 1996). Over years, the effect will contribute to a shortening of the vegetation at higher elevations. Like many other tropical mountains (Downing et al., 2017; Spehn et al., 2006), the higher elevation of Mt. Meru is prone to fire as it is dominated by shrubs and grasses that act as fuel for the wildfire. The last wildfire in this zone occurred in the year 2015 and burned ca. 16% of the area (information from the park management). Fire events are closely connected to climatic

conditions and increase in frequency with decreasing precipitation (Chen et al., 2014; Holden et al., 2018).

Through our systematic way of choosing the study sites in space, we derived the “typical” vegetation of the Eastern slopes of the mountain but possibly missed smaller areas of vegetation with extremely tall trees. Our study observed a maximum tree height of about 20 m in the lower elevations of the study area. However, in some patches of the midelevation (2000–2500 m a.s.l.), there is the existence of dominant *Juniperus-Podocarpus* forests with taller trees of up to 40 m (Beesley, 1972).

4.3 | Floristic composition

Results of a NMDS and permutational MANOVA analysis indicated four species clusters; two in the lower elevation (<2100 m a.s.l.), one in the midelevation (between 2100 and 2500 m a.s.l.), and one at the higher elevation above (>2600 m a.s.l.). All clusters have different species compositions (Table 1), which are shaped by a significant interaction of MAT and MAP.

The two lowland elevation clusters vary in the annual amount of precipitation received. One cluster is subjected to the lower precipitation (warm lowland-low precipitation cluster) dominated by *Euclea divinorum* (41.9%), and the other is subjected to consistently higher precipitation (warm lowland higher precipitation cluster) dominated by *Vepris simplicifolia* (35.0%). This observation of lowland clusters dominated by *Euclea divinorum* and *Vepris simplicifolia* is similar to the observation of Hemp (2006) on the Southern slope of Mt. Kilimanjaro between 1500 and 2200 m a.s.l. The author referred to it as “Lower montane forest.” Hemp (2006) reported that the Lower montane forest was dominated by *Ekebergia capensis*, *Syzygium guineense*, and *Agauria salicifolia*. All dominant species in the Lower montane forest observed by Hemp (2006) on the Southern slope of Mt. Kilimanjaro were also observed in our two lower elevation clusters. The midelevation cluster was characterized by moderate to high precipitation and a moderate temperature. Tree communities were dominated by *Bersama abyssinica* (45.7%). Observation of this wet midelevation cluster is consistent with Hedberg (1951) and Bussmann (2006) who observed this vegetation cluster between 2000 and 2300 m a.s.l. They referred to it as “evergreen subtropical montane forest” and found it dominated by *Olea capensis*, *Cassipourea malosana*, and *Podocarpus latifolius* species. The higher elevation cluster characterized by low temperature and low precipitation was dominated by *Erica arborea* (26.0%) and *Hypericum revolutum* (25.7%). This observation of *Erica arborea*–*Hypericum revolutum* cluster between 2600 and 3400 m a.s.l. is similar to that of Bussmann (2006) on Mount Meru and Hemp (2006) on the southern slope of Mt. Kilimanjaro who referred to it as “Upper montane forest.”

Our results showed unoverlapped vegetation clusters and discontinuity in the vegetation composition. This showed that the vegetation of Mount Meru forms altitudinal zonation similar to that of Mt. Kilimanjaro (Hemp, 2006) and not a continuum as suggested by the data of Hamilton (1975). Our findings prove that climate

TABLE 1 Characteristics of woody plant communities of Mt. Meru, Tanzania, identified by nonmetric multidimensional scaling (NMDS), including dominant species, elevation (m.a.s.l.), species richness, and percentage composition of other species.

Cluster	Lowland-low ppt cluster	Lowland-high ppt cluster	Mid elevation	High elevation
Elevation (m.a.s.l.)	1600–2100	1600–2100	2100–2500	2600–3400
Species	14	15	11	13
Dominant species	<i>Euclea divinorum</i> (41.89%)	<i>Vepris simplicifolia</i> (35.00%)	<i>Bersama abyssinica</i> (45.71%)	<i>Erica arborea</i> (26.00%) <i>Hypericum revolutum</i> (25.67%)
Other species	<i>Bersama abyssinica</i> (6.76%) <i>Casearia battiscombei</i> (2.70%) <i>Dodonaea viscosa</i> (5.41%) <i>Ekebergia capensis</i> (2.70%) <i>Lippia javanica</i> (2.7%) <i>Olea africana</i> (4.05%) <i>Olea capensis</i> (8.11%) <i>Peddiea fischeri</i> (5.51%) <i>Ritigina sp</i> (2.70%) <i>Tabernaemontana ventricosa</i> (1.35) <i>Trichilia emetica</i> (2.70%) <i>Turraea robusta</i> (2.70%) <i>Vepris simplicifolia</i> (10.81%)	<i>Albizia petersiana</i> (1.25%) <i>Casearia battiscombei</i> (5.00%) <i>Croton macrostachyus</i> (2.5%) <i>Dodonaea viscosa</i> (1.25%) <i>Juniperus procera</i> (1.25%) <i>Lepidotrichilia volkensii</i> (1.25%) <i>Olea africana</i> (5.00%) <i>Peddiea fischeri</i> (21.25%) <i>Rauvolfia caffra</i> (3.75%) <i>Syzygium guineense</i> (6.25%) <i>Tabernaemontana stapfiana</i> (7.50%) <i>Tabernaemontana ventricosa</i> (6.25%) <i>Trichilia emetica</i> (1.25%) <i>Euclea divinorum</i> (1.25%)	<i>Maytenus sp</i> (1.90%) <i>Cassipourea malosana</i> (4.76%) <i>Juniperus procera</i> (2.86%) <i>Lepidotrichilia volkensii</i> (5.71%) <i>Olea capensis</i> (2.86%) <i>Podocarpus latifolius</i> (5.71%) <i>Trichilia emetica</i> (2.86%) <i>Vepris simplicifolia</i> (12.38%) <i>Nuxia congesta</i> (14.29%) <i>Xymolus monospora</i> (0.95%)	<i>Agauria salicifolia</i> (4.00%) <i>Bersama abyssinica</i> (0.33%) <i>Crotalaria agatiflora</i> (3.00%) <i>Philippia excelsa</i> (1.00%) <i>Hagenia abyssinica</i> (13.67%) <i>Juniperus procera</i> (3.33%) <i>Myrsine africana</i> (4.67%) <i>Podocarpus sp1</i> (1.33%) <i>Podocarpus latifolius</i> (4.33%) <i>Podocarpus sp2</i> (0.67%) <i>Stoebe kilimandscharica</i> (12.00%)

plays a central role in the distribution of plant species (Svenning & Sandel, 2013) and that climate variables can interactively affect the composition of species communities (Peters et al., 2019; Zhu et al., 2019). From our results of vegetation composition, it has been proved that climate has a strong relation with vegetation composition along an elevational gradient. These can potentially be explained by species-specific climatic niches (Costa et al., 2018). For instance, intolerance to the colder climate in the higher elevations may restrict the occurrence of some species of warm regions (lower elevations) while sensitivity to drought may restrict the occurrence of some species of humid regions. According to this, a larger pool of species can potentially persist in the warm and humid climate (lower elevation) when compared to drier and cold climates in the higher elevations.

The climate data used in this study were derived from a global data base (CHELSA; Karger et al., 2017). While the CHELSA data base provides climate data at a rather high resolution (30arcs) and has been shown to have a high performance or both measures of MAT and MAP, it is, nevertheless, based on models. The modeled values for MAT and MAP may therefore differ to some from field-measured values of MAT and MAP on study plots. A comparison of field-measured data of MAT and MAP from the nearby Mt. Kilimanjaro with predictions of the CHELSA database revealed a high level of correlation (MAT, Pearson correlation coefficient $r = .97$ for MAT and $r = .87$ for MAP; MKP, unpublished data), speaking for a good performance of the CHELSA data in predicting local climatic conditions on mountains in Northern Tanzania.

5 | CONCLUSION

This study described woody plant species richness, vegetation structure, and floristic composition along the eastern slopes of Mt. Meru and showed how these variables vary with changing climate along the elevation gradient. The study has shown a monotonic decrease in species richness similar to Peters et al. (2016) and Cirimwami et al. (2019) observations on neighboring Mt. Kilimanjaro and not hump-shaped pattern as suggested by Kitayama (1992). The observed monotonic decline in the richness of woody plants and in tree height with elevation could be explained by our relatively short gradient from 1600 to 3400 m.a.s.l. and the exclusion of areas of lower elevation that are, however, strongly degraded by anthropogenic activities.

This study has found four vegetation clusters formed by the interaction effect of MAT and MAP. We encourage more studies on vegetation communities as they would help to assess the impact of global climate change on biodiversity. Non-overlapping vegetation clusters formed suggest a vegetation zonation as it was proposed by Hemp (2006) in the neighbouring Mt. Kilimanjaro.

The close correlation between woody plant species richness, tree height, plant species composition, and climate suggests that further vegetation changes are expected as climate change is ongoing. In particular, our finding of an interactive effect of MAT and MAP underpins that the response of montane woody plant communities to temperature increase will depend on the potential changes in rainfall. Our

study can 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. Further, the study would benefit from the inclusion of soil data in its analyses. This will provide an opportunity for future studies in the area.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in figshare at [10.6084/m9.figshare.22723901.v1](https://doi.org/10.6084/m9.figshare.22723901.v1)

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