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Role of topography, soil and climate on forest species composition and diversity in the West Usambara Montane Forests of Tanzania

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Abstract

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Understanding the variables that determine the variation in forest species composition and diversity in tropical montane systems remains a topic for discussion in plant ecology. This is especially true in areas where the topography is complex and forests are vulnerable to human activity. In this study, a set of topographic, soil, and climatic variables were used to determine their effects on the composition and diversity patterns of two forests in the West Usambara Mountains (Tanzania). Two-phase systematic sampling was used to collect vegetation data from 159 sample plots distributed across the forests. An agglomerative hierarchical clustering method was used for forest community classification, and indicator species analysis was used to determine the species significantly associated with forest communities. The influence of environmental variables on forest communities was analysed using canonical correspondence analysis (CCA). Finally, we evaluated diversity patterns by comparing diversity indices (Shannon-Wiener diversity index, evenness, and richness) and beta diversity processes. In total, 7,767 individual trees belonged to 183 species, 132 genera, and 66 families were quantified. We found that (i) the forests of West Usambara can be divided into three different forest communities; (ii) each forest community has a specific set of topographical, soil, and climate variables; (iii) there are significant differences in Shannon diversity and richness indices among communities; and (iv) community composition is mostly influenced by species turnover than by species nestedness. Our study revealed the importance of considering a set of environmental variables related to climate, soil, and topography to understand the variation in the composition and diversity of forest communities in tropical montane forests.

Keywords

beta diversity, canonical correspondence analysis (CCA), indicator species, species richness, tropical mountains

Introduction

Tropical montane forests (TMFs) are important components of global biodiversity hotspots (Mata-Guel et al., 2023). They are characterized by their unique composition of flora and fauna, complex ecological interactions, and high levels of endemism (Brambach et al., 2017). TMFs occur at elevations between 1,000 and 4,000 m above sea

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level in tropical regions worldwide, where they represent a critical resource for local communities and significantly contribute to global carbon storage (Iwashita et al., 2013; Spracklen and Righelato, 2014). The ecological complexity of TMFs is attributed to a combination of factors including topographic heterogeneity (Jiang et al., 2023), climatic variability (Trew and Maclean, 2021), and high levels of endemism (Nery et al., 2023). These factors create a mosaic of microhabitats, each with distinct biotic and abiotic conditions, resulting in high levels of diversity and endemism at multiple scales (Noguerales et al., 2021; Tietje et al., 2022). The unique environmental conditions in TMFs have also led to the evolution of specialized species and communities, making them important sites for studying speciation and evolutionary processes (Trew and Maclean, 2021; Vasconcelos et al., 2022).

However, understanding the environmental variables that influence forest composition and diversity in TMFs remains a topic of discussion in plant ecology (Diogo et al., 2021; Hai et al., 2021; Hofhansl et al., 2020). Multiscale factors are thought to be important for determining forest composition and diversity patterns across these forests (Barczyk et al., 2023). Regional (e.g., climate) and local factors, such as topography and soil, are important drivers of forest composition and diversity in montane forests (Homeier and Leuschner, 2021; Li et al., 2020). For example, topography creates a wide range of microclimates that influence the distribution and abundance of various plant species (Macek et al., 2019; Oldfather and Ackerly, 2019). Soil type and chemistry also play critical roles in shaping the composition of TMFs, with different plant species adapted to specific soil types and their associated nutrient cycles (Dantas de Paula et al., 2021).

In addition to these factors, climate variability is a critical driver of forest composition and diversity in TMFs (Boyle et al., 2021), and is expected to become increasingly important in the face of ongoing climate change (Ntirugulirwa et al., 2023). Climate change is projected to result in warmer temperatures and altered precipitation patterns in tropical regions, leading to changes in moisture availability and nutrient cycling, which will have cascading effects on TMFs (Veintimilla et al., 2019). Therefore, it is important to understand how TMFs respond and adapt to changing climatic conditions, and how these changes may affect forest composition and diversity in the future (Salinas et al., 2021).

Although previous studies have explored the influence of individual environmental variables on montane forest composition and diversity (Báez et al., 2022; Bunyan et al., 2015; Fahey et al., 2016; Homeier, 2010; Lakkana et al., 2002; Lippok et al., 2014; Rawat et al., 2020; Takyu et al., 2002; Zhang et al., 2016), there is a lack of comprehensive research that incorporates the interactive effects of climate, soil, and topography. The Eastern Arc Mountain forests are biodiversity hotspots, renowned for their species richness, endemism, and unique ecological characteristics (Dimitrov et al., 2012; Yessoufou et al., 2012). Within the Eastern Arc Mountain forests, the West Usambara Montane Forests offer an ideal setting for ecological research, with diverse forest communities and a wealth of endemic species (Huang et al., 2003; Rodgers and Homewood, 1982; Tallents et al., 2005). The West Usambara Montane Forests provide a condensed yet representative ecosystem within the Eastern Arc Mountain forests, making them an excellent study site for investigating the influences of climate, soil, and topography on forest composition and diversity. Therefore, this study aims to address this research gap by focusing on the West Usambara mountain forests and pursuing the following objectives: 1) to identify different forest communities in the study area, 2) to evaluate the influences of topography, soil, and climate on forest community composition, and 3) to determine the patterns of alpha diversity between forest communities and the underlying processes contributing to the beta diversity of these communities. It is important to note that this study intentionally excluded human disturbance as a factor in isolating the specific effects of abiotic factors. By focusing solely on climate, soil, and topography, we aimed to gain a clearer understanding of the natural drivers shaping forest composition and diversity in the absence of human-induced influences. This approach allowed us to assess the direct impacts of abiotic factors on the West Usambara mountain forests and provide valuable insights into their ecological dynamics and conservation needs.

Materials and methods

Study area

The West Usambara Montane Forests are located mainly in the Lushoto District, with a smaller area in the Korogwe District in Tanzania. These forests are confined to the Usambara Mountains, which consist of two highland blocks: East Usambara rising up to 1,484 m and West Usambara rising to nearly 2,294 m. These blocks are part of the Eastern Arc Mountains (EAMs), a group of isolated mountains stretching from Southeast Kenya to the Makambako Gap in south-central Tanzania (Fig. 1). The study was carried out in two forests, the Magamba Nature Forest Reserve (MNFR) and the Shagayu Forest Reserve (SFR) (Fig. 1), both located in the West Usambara Mountain block. The MNFR, covering an area of 9,283 ha, is situated at 4°40 S and 38°15'E, with an altitude ranging from 1,650 to 2,300 m above sea level, a mean annual rainfall of 1,200 mm per year, and an annual temperature ranging from 15 °C to 30 °C. The SFR, with an area of 7,830 ha and is located at 4°31'0''S and 38°16'59''E, has an elevation of approximately 2,098 m asl and a mean annual rainfall of 1,000 mm per year (Lovett, 1996).

Vegetation sampling and plant identification

A two-phase, systematic sampling design was used in this study. Grids (225 × 450 m in the MNFR and 350 × 700 m in the SFR) were established during the first phase, with each intersection being a sampling plot. During the field expedition, second-phase plots were selected based on a careful consideration of logistical and practical constraints, including time, resources, and the accessibility

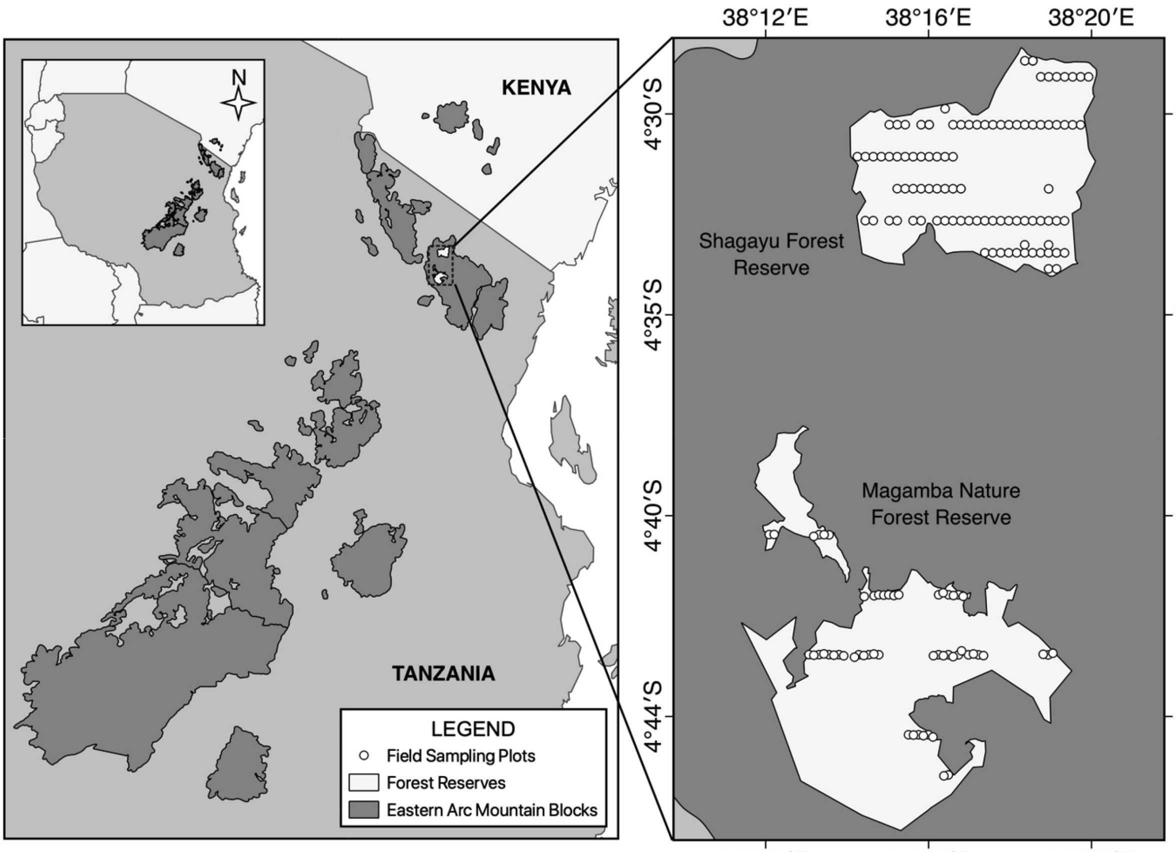

Fig. 1. Shagayu forest (7,830 ha) and Magamba nature forest reserves (9,283 ha) and their localizations within the Eastern Arc Mountains of Tanzania.

of the study sites. A total of 159 circular field-sampling plots (radius = 15 m) were established across both forests (MNFR = 55; SFR = 105). In each plot, individual trees with a diameter at breast height (DBH) ≥ 5 cm were recorded and identified at the species level. The geographical location and elevation were also recorded using a handheld GPS (Garmin 73). For data collection, only trees were measured, whereas other plants, such as climbers, shrubs, and herbs, were excluded.

Environmental data

A total of 28 environmental variables, representing topographic (4), climate (19), and soil (5) variables, were used to determine the linkage between species composition and diversity as explanatory variables (Supplementary Table S1). Apart from elevation, the other topographical variables (slope, aspect, and topographic wetness index) were derived from a digital elevation model downloaded from https://glovis.usgs.com. The bioclimatic variables were extracted from global high resolution (~ 1 km^2) database https://www.worldclim.org. High resolution (~ 250 m) soil variables were downloaded from https://www.soilgrids.org. Pearson's correlation coefficient (r) and variance inflation factor (VIF) were used to assess collinearity between environmental variables. In cases of high collinearity (r ≥ 0.7, VIF ≥ 10), the environmental variable that showed a greater relationship with the explanatory variable was retained (Lolila et al., 2023).

Statistical analyses

All statistical analyses were carried out using R v.4.2.1 (R Core Team, 2022). Species area curves were generated using the R package 'biodiversityR' (Kindt and Kindt, 2023), following the method proposed by Preston (1962). In this study, species area curves were used to examine the relationship between sampling effort and number of species found in each forest. To classify the recorded tree species and sampling sites into different forest communities, we used agglomerative hierarchical clustering analysis with the Ward linkage method. The optimal number of forest communities was determined using a consensus-based algorithm carried out with the 'parameters' package (Lüdecke et al., 2023). Tree species that were significantly associated with the sampling plots for each forest community were identified using indicator species analysis via the 'indicspecies' package (De Caceres et al., 2014). Canonical correspondence analysis ordination (CCA) was then conducted using matrices of species biomass and retained environmental variables to investigate the influence of environmental variables on indicator tree species distribution in each forest community. The axis length (> 4.0) of a detrended correspondence analysis (DCA) was used to identify the suitable constrained ordination method (i.e. CCA). Stepwise forward selection was performed during the CCA ordination to identify significant environmental variables, which was carried out using the 'vegan' package (Oksanen et al., 2008). The Kruskal-Wallis test was used to assess differences in environmental variables across the three forest communities. This non-parametric test was appropriate for our data as it did not meet the assumptions of normality and equal variances. The test was followed by post-hoc analysis using Dunn's test, which allowed for the identification of significant differences within communities.

Alpha diversity indices, particularly the Shannon diversity index (H) (Shannon and Weaver, 1964), species richness (S), and evenness (J) (Pielou, 1966), were also calculated for each forest community using the 'vegan' package in R (Oksanen et al., 2008). These metrics were used to compare the alpha diversity among the three forest communities. The use of these indices is important, as they provide a comprehensive understanding of the diversity within each forest community and can be used to compare diversity between different communities. To compare the diversity indices evaluated among the three communities, generalized linear models (GLM) were conducted with a Gaussian error distribution, except for species richness, in which a Poisson distribution was used. Pairwise comparisons among forest communities were conducted with estimated marginal means using the package 'emmeans' (Lenth et al., 2018). Additionally, we partitioned the Bray-Curtis coefficient (beta diversity, β) into two measurements to test if any of the forest communities are distinct in terms of species turnover (β_{turn}) and nestedness (β_{nest}) (Baselga, 2013) using the 'betapart' package (Baselga and Orme, 2012). These results were used to infer whether the differences in species composition were due to the segregation of different species in different forest communities (turnover) or because one forest community had only a smaller amount of the same species as the other (nestedness). Therefore, if all forest communities have a large number of niche-specialist tree species, a higher β_{turn} is expected. In contrast, when most of the tree species in a forest community are generalists (e.g., found across other forest communities), a higher β_{nest} is expected.

Results

Sampling effort and forest communities

Data on 7,767 individual trees belonging to 183 species, 132 genera, and 66 families were recorded across both forests. In Shagayu FR, 130 species from 108 genera and 59 families were recorded, whereas in the Magamba NFR, there were a total of 113 species belonging to 89 genera and 53 families. The species area curve (Fig. 2) showed that the maximum tree species richness was under-sampled for the Magamba NFR and adequately sampled for the Shagayu FR. It also revealed that the species richness for Shagayu FR reached the asymptote, whereas for Magamba NFR, the species richness was close to the asymptote.

Three forest communities were identified and described using agglomerative hierarchical clustering analysis (Fig. 3). A total of 62 indicator species were identified in the present study. Forest communities were named based on the two most important tree species that occurred in the forest community, using their indicator value (IV) (Table S2). The three forest communities identified were Dombeya burgessiae-Cussonia spicata (DC), Aphloia theiformis-Syzygium cordatum (AS), and Newtonia buchananii-Parinari excelsa (NP) (Fig. 3).

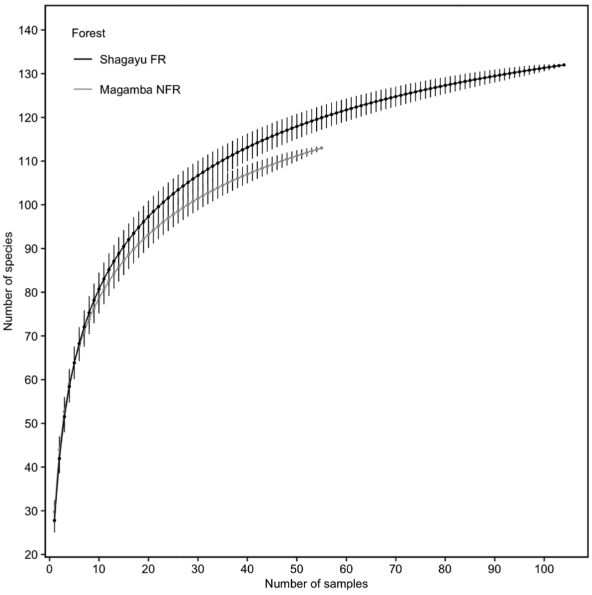

Fig. 2. Species accumulation curves for Shagayu and Magamba forest reserves. The curves depict the expected number of species as a function of sampled area, with the upper and lower bounds representing the 95% confidence intervals.

D. burgessiae-C. spicata (DC) community: This forest community is distributed between 1,734–2,103 m asl. It is represented by 42 plots and has the lowest number of significant indicator species associated with the community (14). *Dombeya burgessiae* Gerrard ex Harv., *Cussonia spicata* Thunb., *Bersama abyssinica* Fresen., *Maesa lanceolata* Forssk, and *Nuxia floribunda* Benth. were the five most dominant indicator species.

A. theiformis-S. cordatum (AS) community: This forest community is distributed over a wider elevation range of 1,683–2,105 m asl, showing a large overlap with that of DC. This community was the largest with 84 plots and was represented by the highest number of significant indicator species (29). Species indicative of this community include *Aphloia theiformis* (Vahl) Benn. And *Syzygium cordatum* Hochst. ex Krauss, *Macaranga kilimandscharica* Pax, *Lasianthus kilimandscharicus* K.Schum., and *Ocotea usambarensis* Engl.

N. buchananii-P. excelsa (NP) forest community: This forest community is distributed in the lowest elevation ranges of 1,425–1,883 m asl. It was the smallest of all communities and was represented by 33 plots and 19 indicator species. Species representative of this community are: *Newtonia buchananii* (Baker) G. C. C. Gilbert & Boutiqu, *Parinari excelsa* Sabine, *Sorindeia madagascariensis* Thouars ex DC., *Leptonychia usambarensis* K. Schum., and *Mimusops kummel* Bruce ex A. DC.

Forest communities and associated environmental variables

Constrained ordination using canonical correspondence

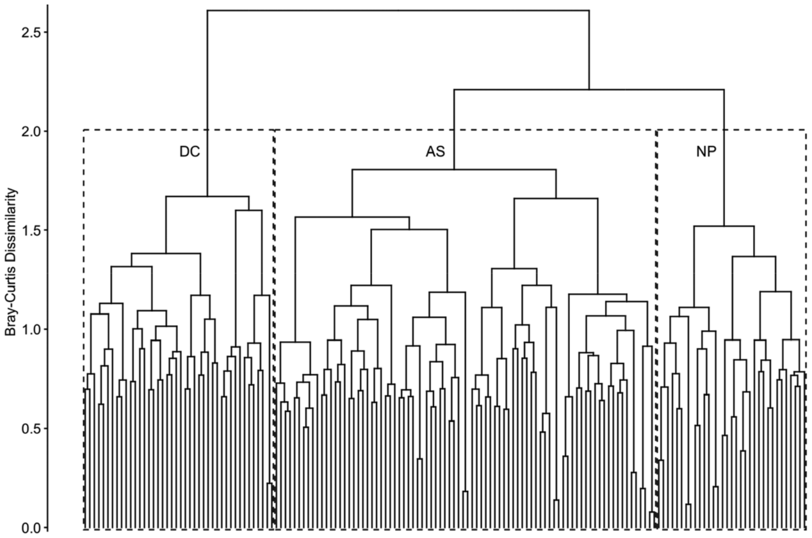

Fig. 3. Hierarchical dendrogram expressing forest communities as a result of clustering analysis. Dashed rectangles indicate the forest communities. DC: Dombeyaburgessiae-Cussoniaspicata, AS: Aphloiatheiformis-Syzygiumcordatum, NP: Newtoniabuchananii-Parinariexcelsa.

analysis (CCA) grouped all sites in a similar manner as in the cluster analysis (Fig. 4). The ordination diagram formed a set of linkages among different forest communities, along with environmental variables. The variables that were retained after performing the collinearity test with a VIF < 10 included topographical, soil, and climate variables, particularly elevation (E), soil nitrogen (N), precipitation in the wettest month (PWM), annual precipitation (AP), topographic wetness index (TWI), soil pH (PH), and mean diurnal range (MDR). The CCA1 and CCA2 axes accounted for 2.74% and 2.10% of the variance, respectively, explained by these significant environmental variables. The results showed that the DC forest community was significantly ($P < 0.001$) associated with E, N, and MDR. The AS community was significantly associated with N and PWM, whereas the NP community was significantly associated with TWI and AP.

All environmental variables (E, N, PWM, AP, TWI, PH, and MDR) differed significantly among forest communities ($p < 0.05$). The DC community had the highest elevation, N, and MDR values, followed in rank order by the AS and NP communities. In contrast, AP and TWI

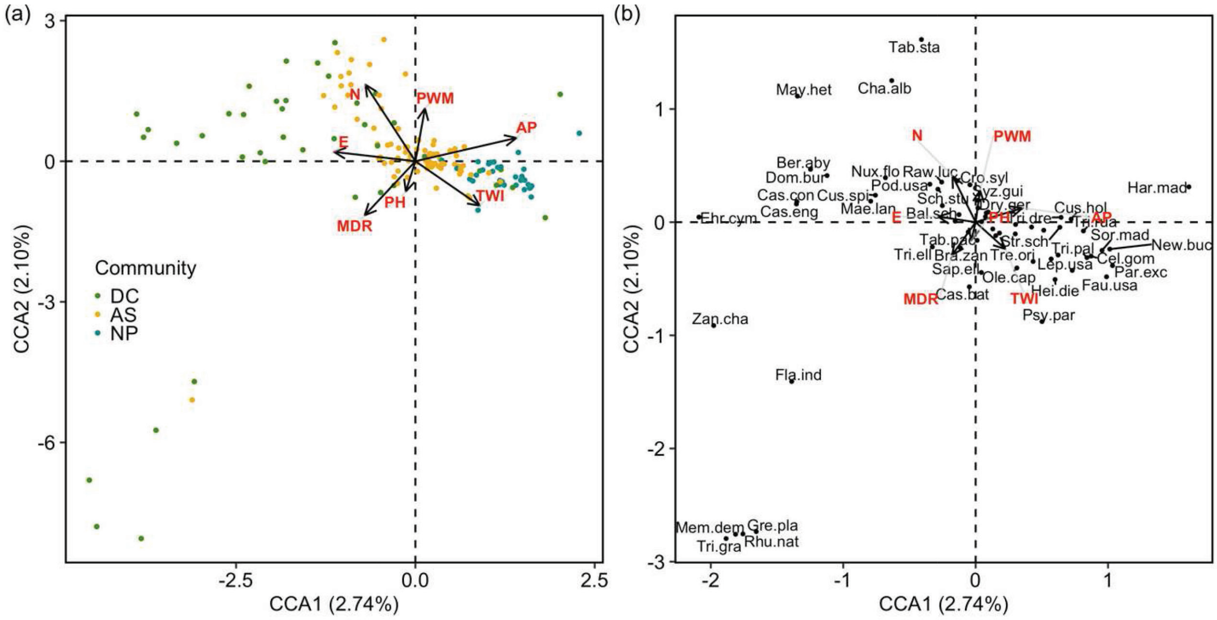

Fig. 4. Canonical correspondence analysis (CCA) ordination diagram showing (a) relationship between environmental variables (elevation [E], soil nitrogen [N], precipitation in wettest month [PWM], annual precipitation [AP], topographic wetness index [TWI], soil pH [PH], and mean diurnal range [MDR]) and forest communities and (b) relationship between environmental variables on indicator tree species distribution in the three forest communities: Dombeya burgessiae-Cussonia spicata (DC), Aphloia theiformis-Syzygium cordatum (AS), Newtonia buchananii-Parinari excelsa (NP). Tree species abbreviations are listed in Table S2.

Table 1. Environmental variable measures (median ± IQR) in each forest community and their differences: Different lowercase letters in rows indicate significantly different medians (Kruskal-Wallis, $p < 0.05$) for elevation (E, metres above sea level m), soil nitrogen (N, ppm), precipitation in wettest month (PWM, mm), annual precipitation (AP, mm), topographic wetness index (TWI, unitless), soil pH (pH, unitless), and mean diurnal range (MDR, °C).

Environmental variable	Forest community			p-value
	DC	AS	NP	
E	1,918.0^{a} ± 183.5	1,893.5^{a} ± 211.00	1,654.0^{b} ± 229.00	<0.001
N	2.49^{a} ± 0.66	2.46^{a} ± 0.55	1.97^{b} ± 0.24	<0.001
PWM	171.0^{ab} ± 16.00	175.0^{a} ± 15.25	165.0^{b} ± 9.00	0.006
AP	919.5^{a} ± 75.75	952.0^{b} ± 68.00	997.0^{c} ± 43.00	<0.001
TWI	9.01^{a} ± 0.90	9.45^{b} ± 0.85	9.62^{c} ± 0.46	0.007
PH	5.45^{a} ± 0.20	5.30^{b} ± 0.30	5.30^{b} ± 0.10	<0.001
MDR	9.56^{a} ± 0.32	9.43^{b} ± 0.32	9.35^{b} ± 0.22	0.006

Forest communities include: Dombeya burgessiae-Cussonia spicata (DC), Aphloia theoformis-Syzygium cordatum (AS), and Newtonia buchananii-Parinari excelsa (NP).

were the highest in the NP community, lowest in DC, and intermediate in AS. Trends in PH were similar to those in N; however, the values were similar in the AS and NP communities. The AS community had the highest PWM, followed by the DC and NP communities, in rank order (Table 1).

Species diversity and pattern

Among the three diversity indices, only Shannon diversity (GLM $\chi^2 = 6.72$, df = 2, $p < 0.05$) and species richness (GLM $\chi^2 = 134.39$, df = 2, $p < 0.001$) were found to be significantly different between forest communities. However, evenness showed no significant differences between forest communities (GLM $\chi^2 = 0.08$, df = 2, p-value > 0.05) (Fig. 5). Shannon diversity was highest in AS (1.79 ± 0.11), followed by NP (1.65 ± 0.165), and lowest in DC (1.34 ± 0.15) (Fig. 5a). D. burgessiae-C. spicata community showed a species evenness of (0.66 ± 0.044), followed by AS (0.66 ± 0.03), and finally (0.60 ± 0.05) (Fig. 5b). Finally, NP had the highest species richness (16.11 ± 1.37), followed by AS (15.95 ± 0.87) and DC (8.59 ± 0.89) respectively (Fig. 5c).

Discussion

Forest communities and associated environmental variables

This study classified Shagayu and Magamba forests into three communities corresponding to a combination of different environmental variables. This demonstrated the role of different environmental variables in the dispersion of

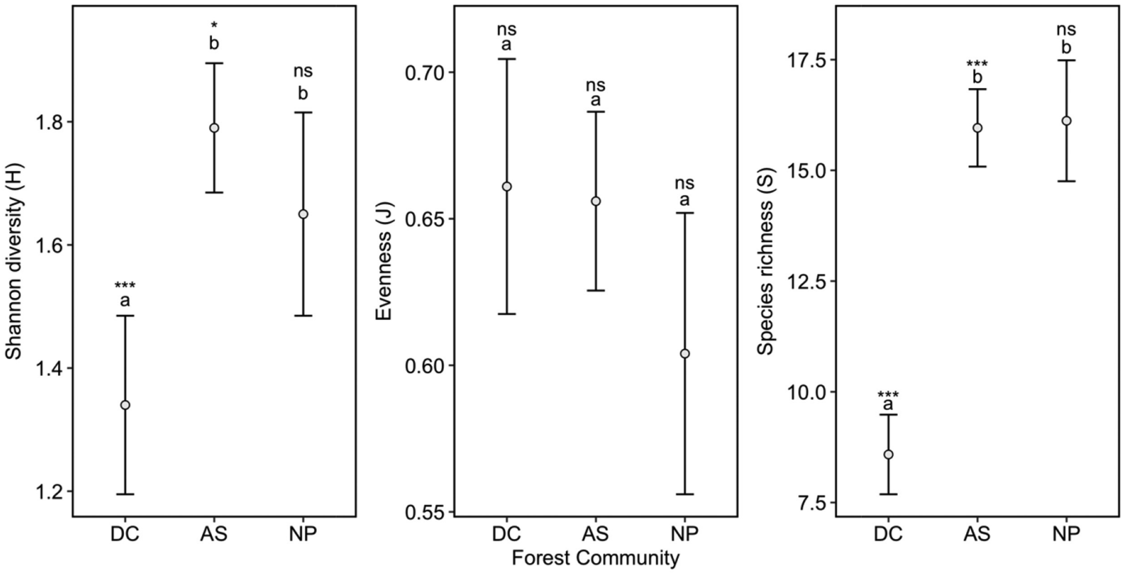

Fig. 5. Variation of alpha diversity indices between the three forest communities of the West Usambara montane forests. Figures represent the diversity index mean (circle) and 95% confidence interval (error bars). Lowercase letters indicate group differences by an estimated marginal mean. DC: Dombeya burgessiae-Cussonia spicata, AS: Aphloia theoformis-Syzygium cordatum, NP: Newtonia bucchananii-Parinari excelsa. p-value: (GLM) with a Gaussian error distribution for Shannon's diversity index and species evenness, Poisson distribution for species richness: $*p < 0.05$, $***p < 0.001$.

Table 2. Beta diversity partitioning results for three forest communities based on Bray-Curtis dissimilarity index

Community	Beta diversity (β)	Turnover (β_{turn})	Nestedness (β_{nest})
DC	0.948	0.889	0.059
AS	0.858	0.783	0.075
NP	0.832	0.747	0.085

these forest communities. Similar findings have been reported in other tropical forests (Latt and Park, 2022; Lolila et al., 2023; Rawat and Negi, 2021); these differences might be due to the unique environmental conditions in each community (Thakur et al., 2022).

The results from the canonical correspondence analysis showed that soil, topographic, and climate variables together played a crucial, although moderate, role in determining species composition in montane forests. For example, CCA identified that the DC and AS forest communities had relatively higher levels of soil nitrogen than NP. Additionally, the AS and NP communities had relatively lower soil pH than DC, indicating that site conditions are important in determining the constitution and distribution of tropical forest communities (Sagar et al., 2003). These findings are further supported by those of Lolila et al. (2023), in which soil pH significantly influenced the composition of forest communities in subtropical montane forests of north-eastern Tanzania.

Topographical variables, particularly elevation and topographic wetness index (TWI), were important variables influencing the species composition of the DC and NP communities at the study sites. The TWI measures the ability of the terrain to retain moisture, which can influence soil moisture and nutrient availability (Kopecký and Čížková, 2010). In general, areas with higher TWI values tended to have wetter soils, which can support a higher diversity of plant species. In tropical ecosystems, the importance of elevation and TWI, as observed in this study, is consistent with known morphological and hydrological landscape factors, which often create distinct forest types (Baldeck et al., 2016; Blanchard et al., 2019; Muscarella et al., 2020).

Additionally, the mean diurnal range (MDR), annual precipitation (AP), and precipitation during the wettest month (PWM) have been shown to significantly influence forest communities. Mean diurnal range is an important factor in determining temperature fluctuations within a given area (Braganza et al., 2004), whereas AP and PWM are important indicators of moisture availability (Li et al., 2016). Several studies have reported on the influence of climatic variables on forest communities. For example, the diurnal temperature range has been found to have a significant influence on the composition of tropical forest communities, despite the narrow annual and diurnal temperature range in the tropics (Punyasena et al., 2008). Similar to our findings, Bhatta et al. (2021) and Nettesheim et al. (2018) documented the influence of AP and PWM in shaping forest composition, with higher values of these variables favouring hygrophytic species growth.

Species diversity pattern

Diversity indices are essential tools for evaluating forest community dynamics and for understanding species diversity patterns (Rubio et al., 2011; Zhao et al., 2022). The results of this study showed that among the three diversity indices measured (Shannon diversity, species richness, and evenness), only Shannon diversity and species richness were significantly different between forest communities, with evenness showing no significant differences. These results indicate that patterns of tree species diversity are related to both large-scale (climate) and small-scale variables (topography and soil), which together determine assemblages of local communities and distribution of species in the forests. The variation in species diversity and richness might be due to the spatial heterogeneity of habitats within forests (Vleminckx et al., 2015; Wiegand et al., 2017). Shannon diversity and richness were the highest in the lower elevation forest communities (AS and NP), which is in line with previous studies that found higher diversity in lower elevation forests (Sharma et al., 2017; Thakur et al., 2022). The low species diversity and richness of the higher-elevation DC forest community could be attributed to harsh environmental conditions that cause physiological stress to the plants (i.e., lower temperature and precipitation), limiting plant growth and regeneration (Zhang et al., 2016).

The finding that species turnover was the main driver of beta diversity in all three forest communities suggests that environmental factors play a crucial role in shaping the forest community composition (Murphy et al., 2016). The strong species-environment relationships observed in this study highlight the importance of considering environmental variables, such as climate, soil nutrients, and topography, when studying forest diversity. These findings are consistent with previous studies that have shown species turnover to be the primary contributor to beta diversity in forest communities (Haq et al., 2021; Murphy et al., 2015; Rahman et al., 2022).

In light of these findings, it is important to consider the potential limitations of this study including aspects such as data collection, sample size, and the chosen statistical analysis technique. For instance, the limitations in data collection methods, such as potential constraints in the selection of environmental variables, could have influenced the accuracy and completeness of our dataset. Additionally, the relatively modest sample size in Magamba forest nature reserve, determined based on practical constraints and available resources, may have impacted the extent to which the identified variables explain the observed variation in species composition and diversity patterns. Furthermore, the chosen statistical analysis technique, while appropriate for our study objectives, may have inherent assumptions or limitations that could affect the precision or generalizability of our findings.

Conclusion

In conclusion, our study sheds light on the ecological characteristics and diversity patterns of tropical montane forests in the West Usambara Mountains. Our findings provide valuable insights into the conservation and management of these ecosystems by identifying distinct forest communities and the abiotic factors driving their composition. The observed differences in the diversity and richness indices between communities highlight the importance of considering local environmental factors when assessing and monitoring biodiversity. Furthermore, the dominance of species turnover over nestedness in shaping community composition underscores the need for conservation efforts that focus on preserving the entire range of species in these forests. Overall, our study contributes to a better understanding of the complex interactions between environmental factors and biodiversity patterns in tropical montane forests, and provides a foundation for future research and conservation efforts in this globally significant biodiversity hotspot.

Conflict of interest

The authors declare no conflicts of interest.

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Author contributions

DLT conceptualized the study, developed the methodology, curated the data, conducted formal analysis, and wrote the original draft. EWM supervised the study, contributed to the conceptualization and methodology, and reviewed and edited the manuscript. SDM conducted the formal analysis, created the visualizations, and wrote the original draft. CJE supervised, reviewed, and edited the manuscript.

Data availability statement

The data used were primarily reflected in this study. Other relevant data and codes are available upon request.

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Supplementary material

Table S1. Environmental variables included in the analysis and their attributes

Category	Environmental variable	Mean	SD	Min	Max
Topographic	Aspect (A, degrees)	173.6	110.2	1.2	353.7
	Elevation (E, m)	1,862.9	166.0	1,433.0	2,180.0
	Slope (S, %)	33.5	15.5	3.9	84.1
	Topographic wetness index (TWI)	9.3	0.8	7.1	11.3
Soil	Soil pH (PH)	5.4	0.2	4.9	5.7
	Soil bulk density (BD, g cm-3)	1,157.5	56.0	997.0	1,300.0
	Soil cation exchange capacity (CEC, cmol kg-1)	16.9	3.3	10.0	26.0
	Soil organic carbon (OC, g kg-1)	35.4	6.0	22.0	56.0
	Soil nitrogen (N, ppm)	2.4	0.5	1.3	3.9
Climatic	Annual mean temperature (AMT, °C)	15.3	1.2	13.6	18.7
	Mean diurnal range (MDR, °C)	9.5	0.3	8.9	10.4
	Isothermality (ISO, %)	63.1	1.1	59.8	64.9
	Temperature seasonality (TS, %)	181.3	6.9	166.0	194.8
	Maximum temperature of warmest month (MaTWM, °C)	23.1	1.1	21.5	26.1
	Minimum temperature of coldest month (MiTCM, °C)	8.1	1.3	6.5	11.6
	Temperature annual range (TAR, °C)	15.0	0.4	14.2	16.2
	Mean temperature of wettest quarter (MTWeQ, °C)	16.6	1.1	14.7	19.5
	Mean temperature of driest quarter (MTDQ, °C)	13.0	1.3	11.3	16.6
	Mean temperature of warmest quarter (MTWaQ, °C)	17.3	1.2	15.6	20.6
	Mean temperature of coldest quarter (MTCQ, °C)	13.0	1.3	11.3	16.6
	Annual precipitation (AP, mm)	949.2	50.5	846.0	1,053.0
	Precipitation in wettest month (PWM, mm)	173.0	8.9	157.0	197.0
	Precipitation in driest month (PDM, mm)	12.3	3.7	7.0	21.0
	Precipitation seasonality (PS)	72.5	4.4	63.1	79.8
	Precipitation in wettest quarter (PWeQ, mm)	397.1	18.3	359.0	434.0
	Precipitation in driest quarter (PDQ, mm)	45.5	11.4	26.0	68.0
	Precipitation in warmest quarter (PWaQ, mm)	303.8	19.3	268.0	339.0
	Precipitation in coldest quarter (PCQ, mm)	47.8	13.5	26.0	78.0

Table S2. Indicator species analysis results for the West Usamabara forests. The species listed in bold had the highest indicator values (IV) and were used to name the forest community that were strongly associated with them.

Scientific name	Code	Cluster	IV	p-val
***Dombey aburgessiae* Gerrard ex Harv.**	**Dom.bur**	**1**	**0.60**	**0.001**
***Cussonia spicata* Thunb.**	**Cus.spi**	**1**	**0.54**	**0.001**
Bersama abyssinica Fresen.	Ber.aby	1	0.53	0.001
Maesa lanceolata Forssk	Mae.lan	1	0.47	0.001
Nuxia floribunda Benth.	Nux.flo	1	0.43	0.006
Cassipourea congensis R.Br. ex DC.	Cas.con	1	0.41	0.002
Rhus natalensis Bernh. ex C. Krauss	Rhu.nat	1	0.35	0.003
Maytenus heterophylla (Eckl. & Zeyh.) N. Robson	May.het	1	0.31	0.012
Memecylon deminutum Brenan	Mem.dem	1	0.31	0.005
Trimeria grandifolia (Hochst.) Warb.	Tri.gra	1	0.31	0.008
Flacourtia indica (Burm.f.) Merr.	Fla.ind	1	0.30	0.012
Ehretia cymosa Thonn.	Ehr.cym	1	0.27	0.019
Grewia platyclada K. Schum.	Gre.pla	1	0.27	0.026
Zanthoxylum chalybeum Engl.	Zan.cha	1	0.27	0.024
***Aphloiat heiformis* (Vahl) Benn.**	**Aph.the**	**2**	**0.76**	**0.001**
***Syzygium cordatum* Hochst. ex Krauss**	**Syz.cor**	**2**	**0.72**	**0.001**
Macaranga kilimandscharica Pax	Mac.kil	2	0.69	0.002
Lasianthus kilimandscharicus K.Schum.	Las.kil	2	0.68	0.003
Ocotea usambarensis Engl.	Oco.usa	2	0.67	0.002
Psychotria goetzei (K.Schum.) E.M.A.Petit	Psy.goe	2	0.66	0.001
Podocarpus usambarensis Pilg.	Pod.usa	2	0.60	0.001
Drypetes gerrardii Hutch.	Dry.ger	2	0.59	0.001
Rapanea melanophloeos (L.) Mez	Rap.mel	2	0.58	0.001
Rawsonia lucida Harv.	Raw.luc	2	0.56	0.003
Vepris nobilis (Delile) Mziray	Vep.nob	2	0.55	0.037
Maytenus acuminata (L.f.) Loes.	May.acu	2	0.54	0.009
Tabernaemontana pachysiphon Stapf	Tab.pac	2	0.54	0.001
Trichocladus ellipticus Eckl. & Zeyh.	Tri.ell	2	0.53	0.001
Pauridiantha paucinervis (Hiern) Bremek.	Pau.pau	2	0.52	0.014
Syzygium guineense (Willd.) DC.	Syz.gui	2	0.51	0.009
Apodytes dimidiata E. Mey. Ex Arn.	Apo.dim	2	0.50	0.002
Scheffler astuhlmannii Harms	Sch.stu	2	0.49	0.001
Balthasaria schliebenii (Melch.) Verdc.	Bal.sch	2	0.49	0.003
Brackenridgea zanguebarica Oliv.	Bra.zan	2	0.46	0.007
Croton sylvaticus Hochst.	Cro.syl	2	0.45	0.019
Garcinia buchananii Baker	Gar.buc	2	0.45	0.005
Chassalia albiflora K.Krause	Cha.alb	2	0.39	0.004
Olea capensis L.	Ole.cap	2	0.36	0.022
Tabernaemontana stapfiana Britten	Tab.sta	2	0.35	0.009
Cassipourea malosana (Baker) Alston	Cas.mal	2	0.32	0.047
Casearia battiscombei R.E.Fr.	Cas.bat	2	0.31	0.023
Macaranga conglomerata Brenan	Mac.con	2	0.29	0.036
Rauvolfia volkensii (K.Schum.) Stapf	Rau.vol	2	0.29	0.025
***Newtonia buchananii* (Baker) G.C.C.Gilbert & Boutiqu**	**New.buc**	**3**	**0.87**	**0.001**
***Parinari excelsa* Sabine**	**Par.exc**	**3**	**0.69**	**0.001**
Sorindeia madagascariensis Thouars ex DC.	Sor.mad	3	0.67	0.001
Leptonychia usambarensis K. Schum.	Lep.usa	3	0.53	0.001
Mimusops kummel Bruce ex A.DC.	Mim.kum	3	0.52	0.002
Strombosia scheffleri Engl.	Str.sch	3	0.52	0.001
*Mammea usambarensis*Verdc.	Mam.usa	3	0.50	0.001
Xymalos monospora (Harv.) Baill.	Xym.mon	3	0.49	0.001
Faurea usambarensis Engl.	Fau.usa	3	0.46	0.001
Harungana madagascariensis Lam. ex Poir.	Har.mad	3	0.42	0.001
Zenkerella capparidacea (Taub.) J.Leonard	Zen.cap	3	0.39	0.004

Table S2. Continued

Scientific name	Code	Cluster	IV	p-val
Trichilia dregeana Sond.	Tri.dre	3	0.39	0.001
Tremaorientalis (L.) Blume	Tre.ori	3	0.37	0.008
Tricalysiapallens Hiern	Tri.pal	3	0.34	0.008
Sapiumellipticum (Hochst.) Pax	Sap.ell	3	0.30	0.009
Tricalysia ruandensis Bremek.	Tri.rua	3	0.29	0.006
Heinsenia diervilleoides K.Schum.	Hei.die	3	0.27	0.022
Celtis gomphophylla Baker	Cel.gom	3	0.25	0.032
Psydrax parviflora (Afzel.) Bridson	Psy.par	3	0.25	0.043