















## Drivers of forest structure and biomass along a climatic gradient in the Soutpansberg, South Africa

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### ABSTRACT

Forest structure plays a key role for providing different ecosystem services in rural regions worldwide. In forests and woodlands of southern Africa, there is a lack of quantitative information on prevailing structures, their abiotic and biotic drivers, as well as how stand characteristics will be affected by climate change. In this study, we established permanent research plots in mature developing stages of representative forests and woodlands occurring along a strong climatic gradient. Effects of site-available soil water and forest type were investigated for relevant dendrometric, as well as structural forest variables. We found site-available soil water having a significantly positive effect on all variables, apart from tree density and the ratio of multi-stem trees. Among the factors influencing site-available soil water, climate had a higher impact than topographical wetness index and soil available water capacity. Studied variables were also strongly influenced by the different forest and woodland types emerging, probably due to different species compositions, survival strategies and fire adaptations. Structural forest variables were revealed to have a positive effect on AGB especially in taller stands having enough space to form multiple canopy layers. In light of climate change with less soil water available and a related ongoing species and biome shift in southern Africa, our findings indicate that in the future, most of the studied forest variables, their related ecosystem functions and services are likely to decrease in the Soutpansberg region. The results of this study could be of use as input data for landscape level modelling, as well as for creating local management policies.

### 1. Introduction

Tropical forests and woodlands on the African continent are home to a broad variety of plant species, forming the habitat and food source for animals of all kinds ranging from insects to megaherbivores. This floral and faunal biodiversity in return is pivotal for providing different ecosystem services (ESS) to the human population, particularly in

remote and rural regions, ranging from provisioning and supporting to regulating and cultural services (Scholes and Biggs, 2004). However, not each forest and woodland provides the same variety and quantity of ESs. Instead, the potential of providing ESs strongly depends on the specific structure of forests and woodlands (Brocknerhoff et al., 2017; Cortés-Calderón et al., 2021; Ehbrecht et al., 2021; Felipe-Lucia et al., 2018).

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Thus, investigating different forest variables is important for quantifying the potential of African forests and woodlands to provide ESs and for designing forest management plans and bio-economic strategies for rural development (Geldenhuis and Vermeulen, 2012). In many areas of biodiverse southern Africa however, no inventories have been conducted so far and field-work-derived quantitative descriptions are lacking. Moreover, environmental factors driving forest variables are strongly affected by current and future climate change conditions, making it important to better understand and predict the impact of different environmental drivers on specific forest variables. In this study we categorized forest variables into dendrometric (e.g., tree density, stocking, deadwood) and structural variables (e.g., stem diameter distribution, regeneration, species diversity) and investigated them within the Soutpansberg region. A so far less studied part of South Africa (Araia, 2019; Mostert et al., 2009) that includes three of the six woodland (savanna) bioregions within the country and two different types of the national forest biome (Mucina et al., 2014), thus representing a much wider landscape making it an interesting study area.

One of the most critical drivers for dendrometric and structural forest variables in mesic to arid regions of Africa, where space and light are not the most limiting growth factors, is the availability of water (Pfadenhauer and Klötzli, 2014; Sankaran et al., 2005), which (among other factors) is a function of three environmental drivers: climate, catchment topography, and soil available water capacity (AWC) (Le Roux et al., 2015; van Tol et al., 2020). The later determined by soil properties such as texture, depth, bulk density, pore size, soil organic matter (SOM) and soil biota (Blum et al., 2020). Recent studies for Africa however show that the 21st century overall will go along with higher mean annual temperatures (MAT) and frequency of heat waves, reduced mean annual precipitation (MAP), and extended dry seasons, resulting in empty water catchment areas, and thus enhanced drought stress for trees (Engelbrecht and Engelbrecht, 2016; IPCC, 2023). Past time series and predictions into the future also reveal a reduced vegetation density, forest cover, and plant health, especially in subtropical southern Africa (Hansen et al., 2013; Lawal et al., 2019), which leads to increased wind & water erosion and changes in quantity and composition of SOM and soil biota (Brevik, 2013; Kardol et al., 2010; Poeplau and Dechow, 2023). As this means that climate change is predicted to shift at least two of the main drivers of future water availability: climate and AWC, more research is needed to understand the influence of site-available soil water on dendrometric and structural forest variables. However, except for the effect of climate on biomass, so far there have been very few studies investigating the influence of site-available water on dendrometric and structural forest variables in southern Africa (Colgan et al., 2012; Godlee et al., 2021; Shackleton and Scholes, 2011).

Apart from site-available soil water, dendrometric and structural forest variables, also depend on the individual forest and woodland type. Forest and woodland types however, have emerged at specific sites not only based on different pedo-climatic conditions like available soil water and nutrient supply, but also as a result of aspect, elevation, local animal-plant interactions, different seed dispersal- and species-specific survival strategies, as well as fire proneness of a specific location (Geldenhuis, 2012). Thus they reflect a range of abiotic and biotic growth conditions, other than available soil water. Due to its diverse environmental conditions, South Africa, hosts nine distinct biomes (Mucina and Rutherford, 2006), with 26 different natural forest, and 87 different woodland types (FAO, 2020a). Studies over the last decades however, have shown that southern Africa, is undergoing nothing less than a severe shift in species composition, resulting in change of forest types and even biomes (Guo et al., 2017; Higgins et al., 2024; Mtsetfwa et al., 2023; Rutherford, et al., 2000). Despite this, studies investigating effects of forest types on stand variables are rare so far for southern Africa (Godlee et al., 2021). Given this background, it is relevant to investigate dendrometric and structural forest variables not only based on the availability of water but also on different forest and woodland types.

Since the Kyoto Protocol in 1997 and the Paris Agreement in 2015, quantifying and monitoring terrestrial biomass and emissions from land-use change have become important (IUCN, 2014; UNFCCC, 2016, 1998). As a result of this, many studies over the last decades have aimed at developing tree species and forest-type specific above-ground biomass (AGB) equations based on dendrometric variables like diameter at breast height (DBH), wood density, and tree height (Chave et al., 2014; Magalhães and Seifert, 2015; Toit et al., 2016). During recent years, however, more and more studies worldwide have also tried to better understand the influence of species diversity and structural heterogeneity on AGB (Ahmed et al., 2022; Godlee et al., 2021; Hilmers et al., 2025). The underlying theory in most of these studies is the niche complementarity hypothesis implying that AGB is driven by species diversity, as only a wide mixture of species with different structural morphology and ecophysiological traits can utilize available resources (light, water, nutrients) most efficiently (Poorter et al., 2015; Tilman et al., 2014). However, some of these studies for Africa so far have reported weak or no positive effect of species diversity on AGB arguing that the relation depends on the study scale, with larger scales tending towards environmental conditions overlying the effect of diversity (Balima et al., 2021; Chisholm et al., 2013; Mensah et al., 2023). Thus, investigating the effect of species and structural diversity on AGB at a regional scale and across a climatic gradient, apart from the well-known effect of dendrometric variables, is of relevance to the question of how AGB is driven by structural forest variables.

The present study, therefore, aims to address the following research questions for dominant forest and woodland types of the Soutpansberg region in South Africa:

(Q - I) How does site-available soil water influence dendrometric and structural forest variables?

(Q - II) How do forest types, in addition to site-available soil water, affect these forest variables?

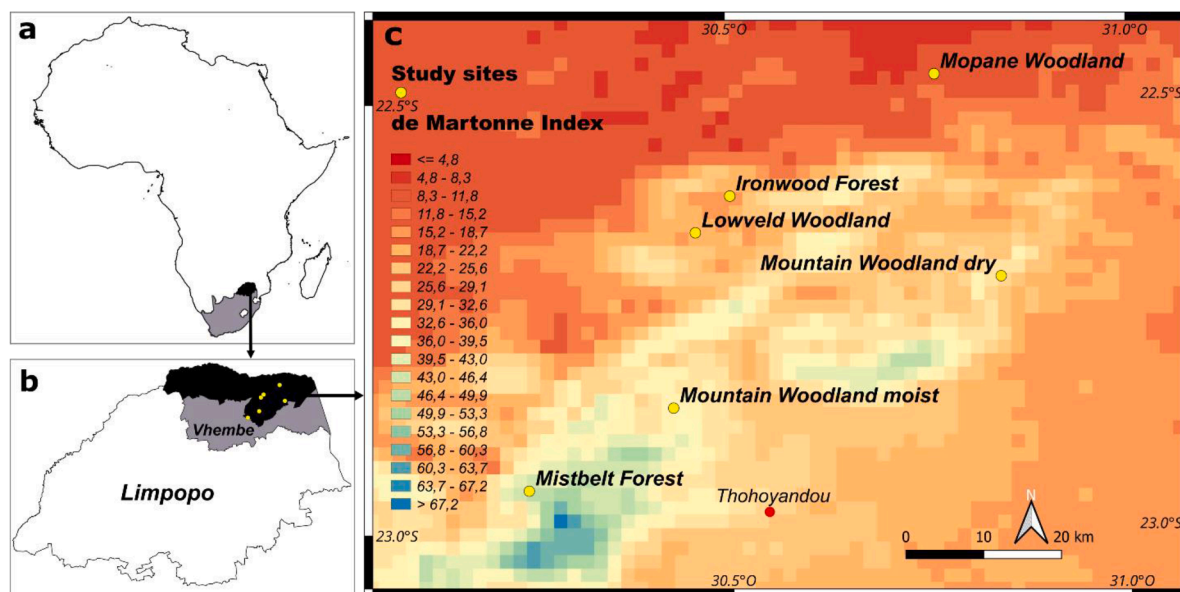
(Q - III) Do structural variables have additional value for predicting AGB apart from dendrometric variables?.

## 2. Material & methods

### 2.1. Study area

The Soutpansberg belonging to the Vhembe Biosphere Reserve, is a unique region within Southern Africa because of its special local climatic conditions. Its tropical climate is dominated by a dry season from May - September and a wet season with summer rainfall between October - April. Our study region across the Soutpansberg is a 60 × 60 km area (comp. Fig. 1). While the southern side at some sites (e.g., Entabeni) receives a mean annual rainfall of >1600 mm, most sites in the north only receive between 300–400 mm per year (Schulze and Lynch, 2007). This strong climatic gradient is unique and due to the east-west orientation of the Soutpansberg mountain range resulting in orographic precipitation. Moisture laden air coming from the Indian Ocean brought inland by the prevailing south-easterly wind systems are prevented from moving westward by the north-south orientated Wolkberg-Drakensberg escarpment, forcing the maritime air masses to move northwards where they meet the Soutpansberg and shed their moisture on the southern side after being uplifted and cooled down (Mostert et al., 2008).

This orographic precipitation gradient of >1000 mm just along an area of 60 km leads to a broad range of available soil water conditions and to a high diversity in species and plant communities. Many of the important South African forest and woodland types can be found in this region within a comparatively small area, which makes it a unique study region. There are woodlands forming 32.8 % of South Africa, as well as indigenous evergreen forests, like Mistbelt Forest and Ironwood Forest covering 0.3 - 0.56 % of the South African land surface (Mucina and Rutherford, 2006; von Maltitz et al., 2003). Among the woodlands there is the Lowveld Woodland having ca. 69,436 km<sup>2</sup> (approx. 17.4 % of South African woodlands), the Mountain Woodland emerging on ca. 30,



**Fig. 1.** (a) Africa with gray (South Africa) and black (Province Limpopo), (b) Province Limpopo with gray (Vhembe District) and black (Municipalities Thulamela and Makhado), (c) Location of the studied forest and woodland types (yellow points) over a climatic gradient (compare de Martonne Index) across the Soutpansberg from southwest to northeast. Red point represents the next bigger city for orientation.

303 km<sup>2</sup> (approx. 7.6 % of South African woodlands) and the Mopane Woodland covering ca. 25,673 km<sup>2</sup> in South Africa (approx. 6.4 % of South African woodlands) (calculated based on numbers of [SANBI \(2021\)](#)), but representing 30 - 35 % of all woodlands in entire Southern Africa (equivalent to an area of ca. 1.5 million km<sup>2</sup>) ([Makhado et al., 2014](#); [Mapaure, 1994](#)). For more information on nomenclature and species composition of the chosen forest and woodland types see also (Table S 9, S 10).

## 2.2. Inventory and data collection

Based on a georeferenced precipitation map ([Schulze and Lynch, 2007](#)), the vegetation field atlas of South Africa ([Mucina et al., 2014](#)) and several pilot studies in 23 locations across the eastern Soutpansberg, one site was chosen respectively for most of the dominant forest types of the study region (from north to south: Mopane Woodland, Ironwood Forest, Lowveld Woodland, Mountain Woodland and Northern Mistbelt Forest). Because Mountain Woodland was the most dominant forest type, two sites, with deviating climate were chosen, one with around 1000 mm (Mountain Woodland moist) and one with approx. 800 mm annual precipitation (Mountain Woodland dry). After getting permissions from local community councils, within each site, five 30 × 30 m plots were selected based on a systematic approach. During field surveys, 15–20 potential plots were ranked between (1 = best and 6 = worst) based on 5 different criteria: slope (the less the better), stands maturity (the more the better), stands uniformity (the more the better), gaps (the less the better), former harvesting (the less the better). Finally, the plots with the lowest total score were selected. Thus, we targeted only on unmanaged, undisturbed forest and woodlands of mature (late climax) successional development stage ([De Cauwer et al., 2016](#)).

Nested rectangular 30 × 30 m plots were laid out and further divided into nine 10 × 10 m subplots (comp. Figure S 1). Each tree (defined as an upright wooden stem with a diameter of ≥ 5 cm at 1.3 m height ([Balima et al., 2021](#); [Geldenhuis, 2005](#)) was numbered and diameter at breast height (DBH), and plot specific stem coordinates were recorded. For the latter, angles and distances were measured by compass and vertex hypsometer, from the corner poles of the centre subplot each. Tree IDs belonging together, being one plant at the rootstock but having multiple stems, were noted. Tree heights and crown diameters of ≥ 30 trees (along the whole DBH range) were measured for each of the 5 most dominant

(by basal area) species in every forest type (comp. Table S 9). For these individual trees, height and crown diameter was measured with a vertex hypsometer, the latter in N/S and E/W direction, using a compass and vertical sighting method ([Pretzsch et al., 2015](#)). Standing and lying deadwood with a diameter ≥ 10 cm was recorded measuring max., mean, min. diameter, and length/ height each ([BMELV, 2011](#); [FAO, 2020b](#)). Additionally, poles (>1 cm <5 cm DBH) and regeneration, divided further into seedlings (≥ 5 cm <0.5 m height) and saplings (≥ 0.5 m height <1 cm DBH), were collected by species and counted within the central 10 × 10 m subplot (comp. Figure S 1). Species identification was based on a classification guide ([van Wyk and van Wyk, 1997](#)), as well as the knowledge of local experts. Local names were translated using botanical dictionaries ([Magwede et al., 2019](#); [van Wyk, 2011](#)). Within the central subplot soil profiles were dug down to parent material or until a depth of 1.5 m (in case of well-developed soils). Horizon depths were separated based on differences in soil morphology. Core samples were collected in each soil horizon respectively, to determine bulk density and soil texture in the laboratory later.

## 2.3. Calculation of dendrometric & structural and environmental variables

In order to assign each tree ID a tree height and a crown diameter based on their individual DBH values, linear regression models were set up for the six forest types and for their 5 dominant tree species each. In case the tree ID belonged to one of these 30 dominant species, the species-specific model was taken; while a pooled, general forest-type-specific model was used if the species was not among the dominant species. Based on the square root mean crown diameter, we calculated the crown projection area (CPA) according to [Pretzsch \(2009\)](#) (comp. Equation S 1). AGB was calculated at single tree level by equations from literature review (comp. Table S 1). While for Mistbelt Forest, Ironwood Forest and Mopane Woodland forest-type-specific AGB equations could be utilized ([Lisboa et al., 2024](#); [Magalhães, 2017](#); [Magalhães and Seifert, 2015](#); [Mensah et al., 2016](#)); for Lowveld and Mountain Woodland, no specific functions could be found and thus, the global equation for tropical forests and woodlands was applied ([Chave et al., 2014](#)). Wood density was taken from a South African data set ([Magalhães et al., 2020](#)). If species could not be found there, we applied the global wood density data base ([Chave et al., 2009](#)). The average was used in case there was

more than one value per species. If there were species without data, we used the mean value of their genus (Mensah et al., 2016), if the genus was absent, the average wood density of the respective forest type was used. Tree volumes were calculated through dividing AGB by wood density. Volume of standing deadwood was obtained by Equation S 4. Volume of lying deadwood wood was approximated with Newton's cone tip following Pretzsch (2009) (comp. Equation S 5).

Canopy cover was computed per plot, based on the CPAs and the stem coordinates (the latter calculated by distances, angles and trigonometric functions) using the package sf objects in R (Pebesma and Bivand, 2023). First, a tree-ID-specific CPA was assigned to each stem position, then overlapping CPAs were merged together in order to remove areas of intersection. Next, this area was clipped out based on the plot boundaries that were determined before. The coefficient of DBH variation (CV-DBH) and mean height variation (CV-height) (comp. Equation S 2), as well as the Shannon Index for quantifying species diversity (comp. Equation S 3) were calculated.

Using the Q-Field App (OPENGIS.ch, 2025) running on an outdoor tablet, plots were described and mapped in the field.  $2 \times 2$  km raster climate data were later added to the Q-Field project taken from: MAP (Schulze and Lynch, 2007), MAT (Schulze and Maharaj, 2007a) and potential evapotranspiration ( $ET_{pot}$ ) (Schulze and Maharaj, 2007b). Then de Martonne Index (dMI) and Aridity Index (AI) were calculated (comp. Equation S 6, S 7). A digital elevation model (DEM) resolution  $30 \times 30$  m provided by the European Space Agency (DEM GLO-30) was downloaded from the Copernicus browser (ESA, 2025), and re-projected into the reference system WGS84/ UTM 36S. Based on this DEM, slope, aspect and the topographical wetness index (TWI) were determined (comp. Equation S 8), by using the Basic Terrain Analyses Tool from the SAGA add-on (Conrad et al., 2015). In order to get the raster values for each plot polygon, the SAGA Raster Statistics for Polygons were used to receive the polygon-wise cell area weighted mean value.

Permanent wilting point (PWP) and drained upper limit (DUL) were used to determine AWC. DUL and PWP were calculated based on pedo-transfer functions for South Africa using bulk density and soil texture (Schulze, 1995). Collected core samples were dried and sieved ( $<2$  mm) to separate rock and soil fractions. Bulk density was determined by the gravimetric method of Blake and Hartge (1982). Soil texture (sand, silt and clay percentage) was quantified based on Stokes' law using the Hydrometer Method of Bouyoucos (1962). In each horizon AWC was calculated and corrected for rock fraction. AWC data of the total soil profile were obtained by summing up single AWCs of each horizon.

## 2.4. Statistics

In order to reduce amount of target variables for the statistical analysis, five dendrometric and five structural forest variables were defined. In case several variables having similar ecological meaning (like dead wood total, lying and standing), these variables were pooled into one group (comp. Figure S 2). In order to account for redundancy between the variables, a correlation matrix and a principal component analysis (PCA) were computed for all variables (comp. Figure S 3, S 4). For each group, only the variable with the highest explanatory power and the lowest correlation with variables from other groups was chosen to represent its group in the further analysis. The selected 10 variables were: tree density, pole density, AGB, mean height, total volume of deadwood, ratio of multi-stem trees, CV-DBH, total regeneration density, canopy cover, Shannon Index.

Data were visually checked for linearity by plotting target variables over explaining variables. Homogeneity of variance and normality of residuals was tested by plotting model residuals vs. fitted values and drawing residual QQ plots. To avoid non-linearity, heterogeneity of variance, and non-normalized distribution of residuals, we applied log transformation to the respective variables. To ensure the same range of values and comparison of effect sizes, independent variables were standardized using z-score normalization after logarithmization. All

calculations were done using the statistical software R 4.4.2 (R Core Team, 2024), and the packages ggplot2 (Wickham, 2016), nlme (Pinheiro and Bates, 2000) and lme4 (Bates et al., 2015).

For investigating Q-I (How does site-available soil water influence dendrometric and structural forest variables?), the following global model was set up to test the effect of the three environmental variables (dMI, AWC, TWI), as well as all their twofold interactions on the 10 forest variables studied:

$$\begin{aligned} \ln(y) = & a_0 + a_1 \times \ln(dMI) + a_2 \times \ln(AWC) + a_3 \times \ln(TWI) + a_4 \\ & \times \ln(dMI) \times \ln(AWC) + a_5 \times \ln(dMI) \times \ln(TWI) + a_6 \times \ln(AWC) \\ & \times \ln(TWI) + \varepsilon \end{aligned} \quad (1)$$

where  $y$  represents the 10 different target variables of our study,  $a_0$  is the intercept,  $a_1, \dots, a_6$  are the slope estimates of the respective model parameters and  $\varepsilon$  reflects the residual error of the model.

For studying Q-II (How do forest types, in addition to site-available soil water, affect these forest variables?), (1) was extended by the parameter forest type covering all six investigated forest and woodland types occurring along the climatic gradient. Forest type was considered as a single effect and in interaction with each of the environmental variables resulting in the second global model:

$$\begin{aligned} \ln(y) = & a_0 + a_1 \times \ln(dMI) + a_2 \times \ln(AWC) + a_3 \times \ln(TWI) + a_4 \\ & \times \text{forest type} + a_5 \times \ln(dMI) \times \ln(AWC) + a_6 \times \ln(dMI) \\ & \times \ln(TWI) + a_7 \times \ln(AWC) \times \ln(TWI) + a_8 \times \ln(dMI) \\ & \times \text{forest type} + a_9 \times \ln(AWC) \times \text{forest type} + a_{10} \times \ln(TWI) \\ & \times \text{forest type} + \varepsilon \end{aligned} \quad (2)$$

where  $y$  are the 10 different target variables,  $a_0$  is the intercept,  $a_1, \dots, a_{10}$  are the slope estimates of the respective model parameters and  $\varepsilon$  reflects the residual error of the model. For answering Q-I and Q-II, final models were selected for each target variable respectively, based on the two global models (Eq. (1) and (2)) using the AIC criterion and the MuMIn package (Bartoń, 2010). Thus accounting for both: model precision, as well as model generalizability and robustness. Tuckey post hoc tests were carried out on the Q-II model predictions in order to conduct pairwise comparisons between the different forest and woodland types. For comparing model accuracy between the selected models of Q-I and Q-II, an ANOVA was performed on the predictions for each of the forest variables.

In order to answer Q-III (Do structural variables have additional value for predicting AGB apart from dendrometric variables?) we set up the third global model:

$$\begin{aligned} \ln(AGB) = & a_0 + a_1 \times \ln(\text{tree number}) + a_2 \times \ln(\text{multistem ratio}) + a_3 \\ & \times \ln(\text{poles}) + a_4 \times \ln(\text{regeneration}) + a_5 \times \ln(\text{height}) + a_6 \\ & \times \ln(\text{canopy cover}) + a_7 \times \ln(\text{deadwood}) + a_8 \\ & \times \ln(\text{VAR dbh}) + a_9 \times \ln(\text{Shannon Index}) + a_{10} \\ & \times \text{forest type} + \varepsilon \end{aligned} \quad (3)$$

where  $a_0$  is the intercept and  $a_1, \dots, a_{10}$ , are the slope estimates of the respective model parameters and  $\varepsilon$  reflects the residual error of the model. The final model for Q-III was selected based on a step-wise procedure, in which the most insignificant explaining variables were removed from the model until all remaining variables showed a significant effect in order to reduce the amount of explanatory variables. Then, interactions were included among those variables left, and based on the AIC criterion, the final model was selected. An ANOVA was performed on the model predictions to compare the results of this resulting model and the respective AGB model of Q-II.

### 3. Results

#### 3.1. Overview of stand characteristics

Table 1 gives an overview of the most important climatic and geological characteristics, as well as dendrometric and structural forest variables per forest type across the climatic gradient. Starting with the climatic characteristics, MAP and dMI values were highest in the Mistbelt Forest gradually decreasing towards the Mopane Woodland, whereas temperature and potential evaporation increased from Mistbelt Forest to Mopane Woodland (Table 1). AWC and soil depth showed maximum values in the Mistbelt Forest and Mopane Woodland and lowest values in the Ironwood Forest and dry Mountain Woodland, with Lowveld Woodland and Mountain Woodland moist being intermediate. TWI did not deviate strongly apart from above average numbers for the Mopane Woodland.

Regarding the dendrometric and structural forest variables, the Mistbelt Forest was among the highest values for all variables apart from the multi-stem tree ratio. Also the moist Mountain Woodland showed high values except of total deadwood. The dry Mountain Woodland instead had the highest number of poles, as well as a high tree density and Shannon Index, while for the other variables, it showed medium values. Ironwood Forest plots revealed the highest tree density and amounts of deadwood (however with strong variation, compare standard error), but the lowest regeneration, pole and Shannon Index values. Mopane and Lowveld Woodland indicated the smallest values for all forest variables, apart from highest multi-stem tree ratios and, in case of the Lowveld Woodland, a medium Shannon Index and CV-DBH (comp.

Figure S 5, S 6).

#### 3.2. Effect of site-available soil water on forest variables (Q-I)

Overall results of the final linear models selected for each forest variable, showed a positive effect of the three drivers of available soil water: climate (dMI), soil (AWC) and catchment topography (TWI) on all investigated forest variables except for tree density and the ratio of multi-stem trees (Fig. 2).

While density is positively affected by dMI, but negatively by AWC (Fig. 2a), the ratio of multi-stem trees is influenced negatively by dMI resulting in a decline with increasing dMI (Fig. 2f). Apart from this, all other variables were positively affected by increasing dMI. Mean height, AGB, canopy cover and CV-DBH showed higher values under above average AWC (solid line), than under average AWC (dashed line), than with less beneficial AWC (dot-dashed line) (Fig. 2c, d, i, g). TWI had its strongest effect on regeneration (Table 2). There were also interactions between the different environmental drivers. While the interaction between AWC and TWI had a positive effect on canopy cover and AGB, the interaction between dMI and AWC revealed a positive effect on mean height, AGB as well as canopy cover (comp. Table 2). Table S 4 provides equations that predict studied variables based on soil depth instead of AWC.

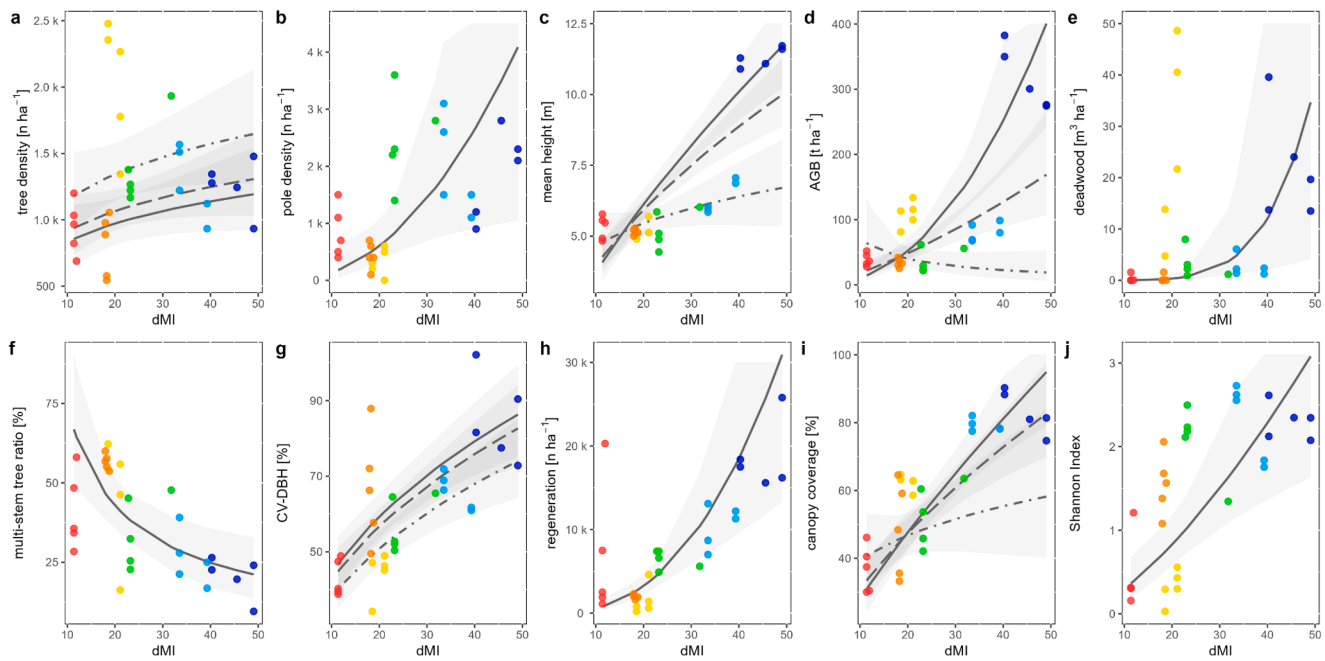
#### 3.3. Effect of site-available soil water and forest type on forest variables (Q-II)

We found a strong overall effect of forest types in relation to the

**Table 1**

Overview of forest inventory variables for the five forest types along the climatic gradient. All values are plot averages per hectare ( $\pm$ standard error): MAP = mean annual precipitation; MAT = mean annual temperature; dMI = de Martonne Index,  $ET_{pot}$  = potential evapotranspiration; Soil depth = depth down to parent rock (max. 1.5 m); AWC = available water capacity; TWI = topographical wetness index; stand density = number of stems with DBH >5 cm; Mean DBH = arithmetic mean of plot diameters; Mean height = arithmetic mean of plot tree heights;  $D_q$  = quadratic mean diameter;  $H_q$  = height of  $D_q$ ;  $H_{95}$  = 95 % quantile of plot tree heights (for remote sensing applications); BA = basal area; AGB = above-ground biomass (volume x basic wood density); volume = AGB/ basic wood density; Lying & standing dead wood = volume of dead wood >10 cm diameter (lying + standing = total deadwood); Ratio of multi-stem trees = share of trees with more than one stem; Poles = DBH >1 cm and <5 cm; Seedlings = height  $\geq$  5 cm <0.5 m; Saplings = height  $\geq$  0.5 m DBH <1 cm (seedlings + saplings = total regeneration); Canopy cover = area inside the plot covered by crowns (without overlaps); CV-DBH and CV-height = coefficient of variation calculated from DBH and height at plot level. Arranged according to descending dMI from left to right.

	Mistbelt Forest	Mountain Woodland moist	Mountain Woodland dry	Ironwood Forest	Lowveld Woodland	Mopane Woodland
<b>Climatic variables</b>						
MAP [mm]	1233.4 ( $\pm$ 54.1)	1074.4 ( $\pm$ 44.3)	793.6 ( $\pm$ 59.9)	622 ( $\pm$ 20.8)	562.6 ( $\pm$ 4.8)	382.2 ( $\pm$ 3.2)
MAT [ $^{\circ}$ C]	17.5 ( $\pm$ 0.0)	20.0 ( $\pm$ 0.0)	21.9 ( $\pm$ 0.2)	21.0 ( $\pm$ 0.1)	20.8 ( $\pm$ 0.0)	23.3 ( $\pm$ 0)
$ET_{pot}$ [mm]	1948.8 ( $\pm$ 6.2)	2020.8 ( $\pm$ 1.4)	2097.6 ( $\pm$ 4.6)	2131.3 ( $\pm$ 5.6)	2167.3 ( $\pm$ 5.6)	2219.8 ( $\pm$ 0.4)
dMI	44.9 ( $\pm$ 2.0)	35.8 ( $\pm$ 1.4)	24.8 ( $\pm$ 1.7)	20.1 ( $\pm$ 0.6)	18.2 ( $\pm$ 0.2)	11.5 ( $\pm$ 0.1)
<b>Geological variables</b>						
soil depth [m]	1.37 ( $\pm$ 0.1)	0.76 ( $\pm$ 0.2)	0.38 ( $\pm$ 0.16)	0.33 ( $\pm$ 0.0)	1.05 ( $\pm$ 0.2)	1.19 ( $\pm$ 0.2)
AWC [mm]	144.2 ( $\pm$ 18.1)	60.0 ( $\pm$ 26.6)	19.3 ( $\pm$ 12.3)	9.2 ( $\pm$ 1.0)	64.3 ( $\pm$ 23.5)	127.8 ( $\pm$ 26.4)
TWI	6.47 ( $\pm$ 0.3)	5.88 ( $\pm$ 0.2)	6.68 ( $\pm$ 0.2)	6.34 ( $\pm$ 0.1)	7.19 ( $\pm$ 0.3)	10.67 ( $\pm$ 1.2)
<b>Dendrometric variables</b>						
tree density [n ha $^{-1}$ ]	1255.6 ( $\pm$ 89.9)	1271.1 ( $\pm$ 119.1)	1393.3 ( $\pm$ 139.4)	2044.4 ( $\pm$ 211.5)	808.9 ( $\pm$ 104.7)	942.2 ( $\pm$ 87.7)
pole density [n ha $^{-1}$ ]	1860 ( $\pm$ 353.0)	1960 ( $\pm$ 379.0)	2460 ( $\pm$ 362.8)	320 ( $\pm$ 106.7)	440 ( $\pm$ 103.0)	840 ( $\pm$ 204.0)
mean DBH [cm]	18.6 ( $\pm$ 0.3)	12.5 ( $\pm$ 0.6)	9.6 ( $\pm$ 0.4)	13.4 ( $\pm$ 1.0)	11.6 ( $\pm$ 0.3)	10.9 ( $\pm$ 0.7)
$D_q$ [cm]	24.5 ( $\pm$ 1.0)	14.9 ( $\pm$ 0.6)	11.1 ( $\pm$ 0.6)	14.6 ( $\pm$ 1.1)	13.9 ( $\pm$ 0.4)	11.9 ( $\pm$ 0.8)
mean height [m]	11.3 ( $\pm$ 0.2)	6.4 ( $\pm$ 0.3)	5.3 ( $\pm$ 0.3)	5.2 ( $\pm$ 0.1)	5.1 ( $\pm$ 0.0)	5.3 ( $\pm$ 0.2)
$H_q$ [m]	13.5 ( $\pm$ 0.2)	6.8 ( $\pm$ 0.1)	5.0 ( $\pm$ 0.1)	5.5 ( $\pm$ 0.2)	5.7 ( $\pm$ 0.1)	5.7 ( $\pm$ 0.2)
$H_{95}$ [m]	18.5 ( $\pm$ 0.5)	9.9 ( $\pm$ 0.4)	7.4 ( $\pm$ 0.5)	6.7 ( $\pm$ 0.3)	7.3 ( $\pm$ 0.1)	7.4 ( $\pm$ 0.4)
BA [m $^2$ ha $^{-1}$ ]	58.8 ( $\pm$ 5.1)	21.7 ( $\pm$ 1.0)	13.6 ( $\pm$ 2.1)	33.1 ( $\pm$ 1.8)	12.3 ( $\pm$ 1.8)	10.2 ( $\pm$ 0.8)
volume [m $^3$ ha $^{-1}$ ]	626.8 ( $\pm$ 73)	129.2 ( $\pm$ 7.7)	64.9 ( $\pm$ 14.9)	138.2 ( $\pm$ 11.2)	58.5 ( $\pm$ 7.9)	42.4 ( $\pm$ 4.6)
AGB [t ha $^{-1}$ ]	316.7 ( $\pm$ 21.4)	81.5 ( $\pm$ 6.1)	38.4 ( $\pm$ 8.4)	108.7 ( $\pm$ 8.7)	33.5 ( $\pm$ 2.8)	38.7 ( $\pm$ 4.3)
lying deadwood [m $^3$ ha $^{-1}$ ]	9.2 ( $\pm$ 3.5)	1.4 ( $\pm$ 0.3)	1.5 ( $\pm$ 0.8)	9.0 ( $\pm$ 4.7)	0.3 ( $\pm$ 0.3)	0.3 ( $\pm$ 0.3)
standing deadwood [m $^3$ ha $^{-1}$ ]	12.9 ( $\pm$ 2.0)	1.3 ( $\pm$ 1.1)	1.6 ( $\pm$ 0.6)	16.8 ( $\pm$ 4.8)	0.0 ( $\pm$ 0.0)	0.0 ( $\pm$ 0.0)
<b>Structural variables</b>						
ratio of multi-stem trees [%]	20.5 ( $\pm$ 2.9)	26.0 ( $\pm$ 3.8)	34.7 ( $\pm$ 5.1)	47.0 ( $\pm$ 8.1)	56.7 ( $\pm$ 1.1)	41.0 ( $\pm$ 5.4)
saplings [n ha $^{-1}$ ]	7660 ( $\pm$ 1893.3)	4760 ( $\pm$ 754.1)	3640 ( $\pm$ 132.7)	300 ( $\pm$ 83.7)	1080 ( $\pm$ 159.4)	780 ( $\pm$ 153.0)
seedlings [n ha $^{-1}$ ]	11,040 ( $\pm$ 1609.8)	5700 ( $\pm$ 1525.5)	2740 ( $\pm$ 560.9)	1220 ( $\pm$ 752.0)	880 ( $\pm$ 190.8)	5880 ( $\pm$ 3448.1)
canopy cover [%]	83.1 ( $\pm$ 2.8)	79.1 ( $\pm$ 0.8)	53.1 ( $\pm$ 4.1)	62.4 ( $\pm$ 1.0)	48.2 ( $\pm$ 6.2)	36.9 ( $\pm$ 3.1)
CV-DBH [%]	84.9 ( $\pm$ 5.2)	66.0 ( $\pm$ 2.1)	57.0 ( $\pm$ 3.3)	44.3 ( $\pm$ 2.6)	66.7 ( $\pm$ 6.5)	43.0 ( $\pm$ 2.1)
CV-height [%]	33.5 ( $\pm$ 1.8)	28.0 ( $\pm$ 1.1)	25.3 ( $\pm$ 1.9)	16.3 ( $\pm$ 1.1)	21.3 ( $\pm$ 1.2)	22.5 ( $\pm$ 1.8)
Shannon Index	2.30 ( $\pm$ 0.1)	2.30 ( $\pm$ 0.2)	2.07 ( $\pm$ 0.2)	0.32 ( $\pm$ 0.1)	1.55 ( $\pm$ 0.2)	0.46 ( $\pm$ 0.2)



**Fig. 2.** Variable-specific model predictions depending on climate dMI = de Martonne Index. In case AWC = available water capacity and TWI = topographical wetness index were part of the final model, they were set to average. In case AWC had a significant effect: solid, dashed and dot-dashed lines represent the 3rd quantile, the mean and the 1st quantile of the AWC respectively. Gray buffers are the 95 % confidence interval for the predicted lines each. Raw data points represent plots ( $n = 30$ ). Colours signify different forest types red = Mopane Woodland, orange = Lowveld Woodland, yellow = Ironwood Forest, green = Mountain Woodland dry, light blue = Mountain Woodland moist, blue = Mistbelt Forest). Variables include: a (tree density,  $k =$  thousand), b (pole density,  $k =$  thousand), c (mean height), d (above-ground biomass), e (deadwood volume), f (multi-stem tree ratio), g (coefficient of variation DBH), h (regeneration,  $k =$  thousand), i (canopy cover), j (Shannon Index).

**Table 2**

Results of selected models (based on Eq. (1)) for each of the 10 forest variables. Given are coefficient estimates of intercepts and predicting model variables (dMI, AWC and TWI), as well as their interactions. Standard errors are in brackets. Significance levels are shown with stars ( $p < 0.05 = *$ ,  $p < 0.01 = **$ ,  $p < 0.001 = ***$ ) and in superscript numbers (in case of close significance).  $R^2$  Adj. = adjusted R-squared (coefficient of determination); AIC = Akaike Information Criterion;  $F = F$ -value; RMSE = Root-Mean-Square-Error. Note that model parameters were standardized (z-score normalization) and logarithmized before. See Table S 3 and S 4 for unscaled model estimates.

	Tree density	Pole density	Mean height	AGB	Deadwood	Multi-stem tree ratio	CV-DBH	Regeneration	Canopy cover	Shannon Index
<b>Intercept</b>	7.094*** (±0.059)	6.659*** (±0.258)	1.806*** (±0.022)	3.940*** (±0.110)	-0.292 (±0.538)	3.635*** (±0.086)	4.063*** (±0.032)	8.404*** (±0.159)	3.951*** (±0.040)	0.043 (±0.161)
<b>dMI</b>	0.105 <sup>0.091</sup> (±0.060)	0.981* (±0.360)	0.207*** (±0.038)	0.257 <sup>0.085</sup> (±0.143)	2.387*** (±0.547)	-0.382*** (±0.094)	0.193*** (±0.033)	1.155*** (±0.222)	0.220*** (±0.052)	0.673*** (±0.164)
<b>AWC</b>	-0.178** (±0.060)		0.106*** (±0.027)	0.325** (±0.108)			0.084* (±0.033)		0.025 (±0.040)	
<b>TWI</b>		0.654 <sup>0.081</sup> (±0.360)	0.111* (±0.040)	-0.345 (±0.212)		-0.008 (±0.139)		0.639** (±0.222)	-0.185* (±0.078)	
<b>dMI × AWC</b>			0.124** (±0.041)	0.785*** (±0.164)					0.132* (±0.060)	
<b>dMI × TWI</b>						0.166 <sup>0.068</sup> (±0.087)				
<b>AWC × TWI</b>				0.716** (±0.196)					0.255** (±0.072)	
$R^2$ Adj.	0.244	0.158	0.841	0.741	0.384	0.485	0.588	0.472	0.767	0.354
AIC	447.4	510.2	72.3	297.3	136.4	238.9	229.4	585.9	225.4	84.1
F	5.674	3.712	39.489	17.593	19.066	10.121	21.691	13.987	20.118	16.891
RMSE	0.30	1.34	0.11	0.39	2.84	0.32	0.17	0.83	0.14	0.85

effects of the three drivers of available soil water. While for every studied variable the parameter forest type was part of the final model, for the variables: tree density, CV-DBH, regeneration and Shannon Index, forest type was even the only parameter of the final model respectively (Table S 5). Comparison of the first and second global model based on quality parameter (Table 3), as well as ANOVA results (Table S 6) revealed that including forest type as an additional model parameter significantly improved model predictions for all forest variables.

Post hoc tests of predicted model results for the variables canopy

cover, AGB, deadwood, number of poles, mean height and multi-stem tree ratio, showed significant differences between most of the forest types (Fig. 3I, D, E, B, C, F). Model predictions for canopy cover, AGB, deadwood, CV-DBH and Shannon Index, gradually reduced from Mistbelt Forest towards Lowveld and Mopane Woodland, while this is opposite for the ratio of multi-stem trees (Fig. 3F). Ironwood Forest however stood out in these patterns, having higher AGB, canopy cover and deadwood values, but lower Shannon Index and regeneration (Fig. 3D, I, E, J, H). Mopane Woodland and Ironwood Forest had overall lowest values for CV-DBH and Shannon Index (Fig. 3G, J). Mistbelt

**Table 3**

Comparisons of model improvements between: without forest types (Q-I/ Eq. (1)) and with forest types as a fixed effect (Q-II/ Eq. (2)). R<sup>2</sup> Adj. = adjusted R-squared (coefficient of determination); AIC = Akaike Information Criterion; F = F-value; RMSE = Root-Mean-Square-Error.

	Tree density	Pole density	Mean height	AGB	Deadwood	Multi-stem tree ratio	CV-DBH	Regeneration	Canopy cover	Shannon Index
<b>Eq. (1)(Q-I)</b>										
R <sup>2</sup> Adj.	0.244	0.158	0.841	0.741	0.384	0.485	0.588	0.472	0.767	0.354
AIC	447.4	510.2	72.3	297.3	136.4	238.9	229.4	585.9	225.4	84.1
F	5.674	3.712	39.489	17.593	19.066	10.121	21.691	13.987	20.118	16.891
RMSE	0.30	1.34	0.11	0.39	2.84	0.32	0.17	0.83	0.14	0.85
<b>Eq. (2) (Q-II)</b>										
R <sup>2</sup> Adj.	0.605	0.811	0.964	0.926	0.748	0.812	0.736	0.670	0.939	0.706
AIC	430.3	471.2	29.7	260.6	113.6	213.8	218.6	574.3	188.8	63.9
F	9.902	12.317	112.851	61.189	15.346	12.364	17.151	12.753	38.339	14.903
RMSE	0.21	0.52	0.05	0.20	1.65	0.16	0.13	0.62	0.06	0.53

Forest however showed values being higher by an order of magnitude compared to other forest types for AGB, regeneration, deadwood and mean height (comp. Fig. 3D, H, E, C).

### 3.4. Influence of dendrometric and structural forest variables on AGB (Q-III)

While the dendrometric variable mean height has the strongest influence between the three model parameters within the selected model for Q-III, the structural variables canopy cover and CV-DBH overall also had a significant and positive influence on the predicted AGB (comp. Table S 7). When setting the mean height to the forest type specific average respectively, the influence of CV-DBH was present for all forest types (Fig. 4). In the case of Lowveld Woodland, Mopane Woodland and Mountain Woodland dry, where canopy cover differed considerably between the individual plots (compare canopy cover standard errors in Table 1), the predicted AGB values varied depending on the chosen canopy cover level.

As shown in Fig. 5, the effect of CV-DBH and canopy cover changed depending on height. A stand with a CV-DBH of 70 %, a canopy cover of 78 % and a below average (1st quantile) height, revealed a AGB of 60.2 t ha<sup>-1</sup>, whereas a stand with the same CV-DBH and canopy cover values but an above average (3rd quantile) height, showed a AGB of 82.3 t ha<sup>-1</sup>, which represents an increase of 36.7 %.

## 4. Discussion

### 4.1. Effect of site-available soil water (Q-I)

Our analyses found that site specific availability of water had a strong positive influence on the dendrometric variables: mean height, pole density, AGB and volume of dead wood, as well as on the structural variables: regeneration, canopy cover, tree species diversity and CV-DBH (Q-I, Fig. 2, Table 2). Our findings for the Soutpansberg region therefore are in line with earlier studies reporting higher tree densities, BAs, AGBs, as well as tree heights with increasing MAP in other parts of Africa (Ganamé et al., 2019; Mureva et al., 2024; Scholes et al., 2002; Shackleton and Scholes, 2011). Along with the increase of these dendrometric variables, the amount of deadwood also gets enhanced (Shackleton, 1998). Large scale studies over different African countries reveal that not only canopy cover and woodland biodiversity increase with rainfall (Davies et al., 2023; Favier et al., 2012; O'Brien, 1993), but also structural variation in diameter and height (Godlee et al., 2021). This holds true also for survival rates of seedlings, established regeneration and number of recruitment stems within the pole size (Joubert et al., 2013; Mensah et al., 2014; Shackleton and Scholes, 2011).

Among the three main drivers of soil water in this study DMI was not only part of the selected final models for each of the structural and dendrometric variables, but overall also had stronger effect sizes than AWC and TWI (Table 2, Table S 2), which both points on the importance of MAP and MAT for the availability of water and the studied stand

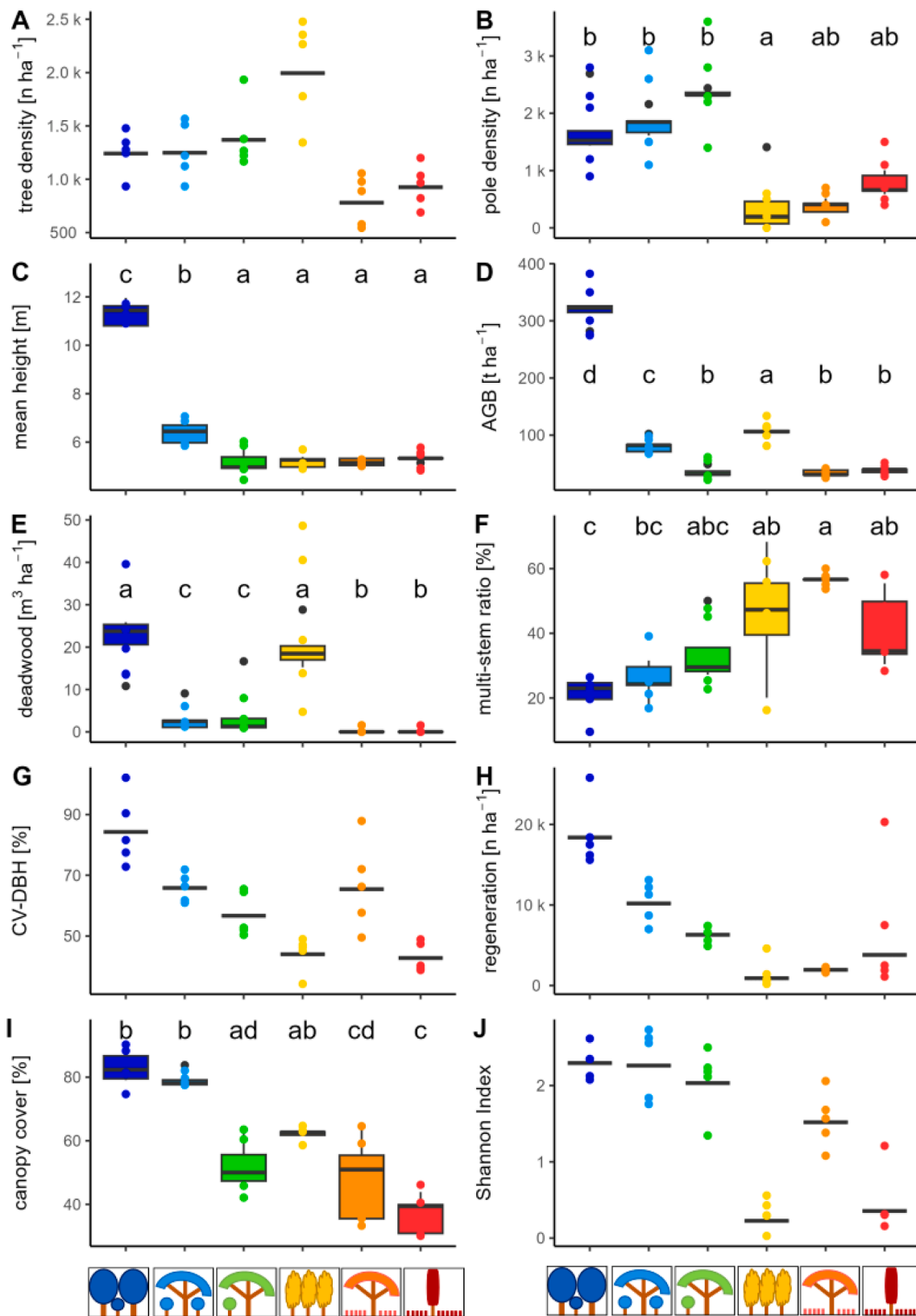
characteristics. This is in line with other studies drawing the picture that (up to a certain point of water saturation) climate is the most important environmental variable for tree and forest development in tropical Africa, setting the frame within which soil, topography, herbivores and fire than can turn potential into reality of a certain site (De Cauwer et al., 2016; Favier et al., 2012; Sankaran et al., 2005).

For understanding the full impact of site-available soil water on different forest variables, apart from the single effects, the interactions between TWI, AWC and dMI also played a key role, as can be seen by change of slopes depending on different AWC levels (Fig. 2c, d, i) and by the strong effects of dMI x AWC, as well as AWC x TWI in terms of mean height, AGB and canopy cover (Table 2). The strong link between AWC and the two other drivers can be explained by the fact, that suitable catchment topography and high rainfalls without a medium to hold back water and make it available also days and weeks after the rain event is of low use for trees (Blum et al., 2020). The explanation why this holds true not only for dendrometric, but also for structural variables might be that sites with a high AWC provide space for a deep and dense root system, which in return enables mechanical stability and enhances the possibility for water and nutrient uptake (Matyssek et al., 2010). These belowground factors however are a precondition for trees to grow tall, develop strong canopies, get more light for photosynthesis and accumulate more AGB. Along with increasing canopy cover and growth rates however, competition and dominance of single trees also gets enhanced, resulting in a stronger structural differentiation within the stand, the effect of out-shading and higher amounts of deadwood.

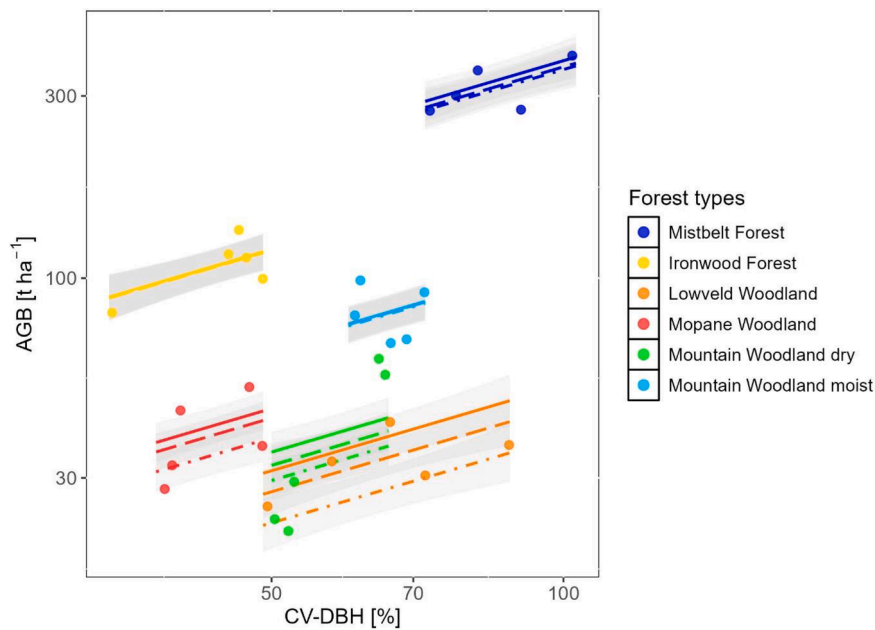
Our study revealed that factors driving available soil water can also have an insignificant or negative effect on some forest variables, as it was the case for the density (AWC) and the multi-stem tree ratio (dMI). In terms of density, most studies found that tree density in African forests and woodlands increases with rainfall (Ganamé et al., 2019; Ngoma et al., 2018; Shackleton and Scholes, 2011). But in line with our results, there are also studies reporting higher tree densities at sites with reduced soil water available (Mureva et al., 2024; Taonda et al., 2024). This could be due to favourable site conditions leading to fast growth of few adapted species resulting in low stem numbers, whereas growth rates and self-thinning dynamics under poor soil conditions are slower, thus keeping density high even in advanced (climax) development stages (Westoby, 1984). Regarding the multi-stem tree ratio, our findings were similar to other results from South Africa also revealing higher branching rates and numbers of multi-stem trees in arid compared to mesic environments (Archibald and Bond, 2003). A reason for this could be that storing resources in belowground rhizomes and using vegetative regeneration (re-sprouting) can serve as a survival strategy for trees growing under arid conditions where damages from drought and fire occur frequently (Bellingham and Sparrow, 2000; Bond and Midgley, 2003; Mlambo and Mapaire, 2006).

### 4.2. Effect of site-available soil water and forest type (Q-II)

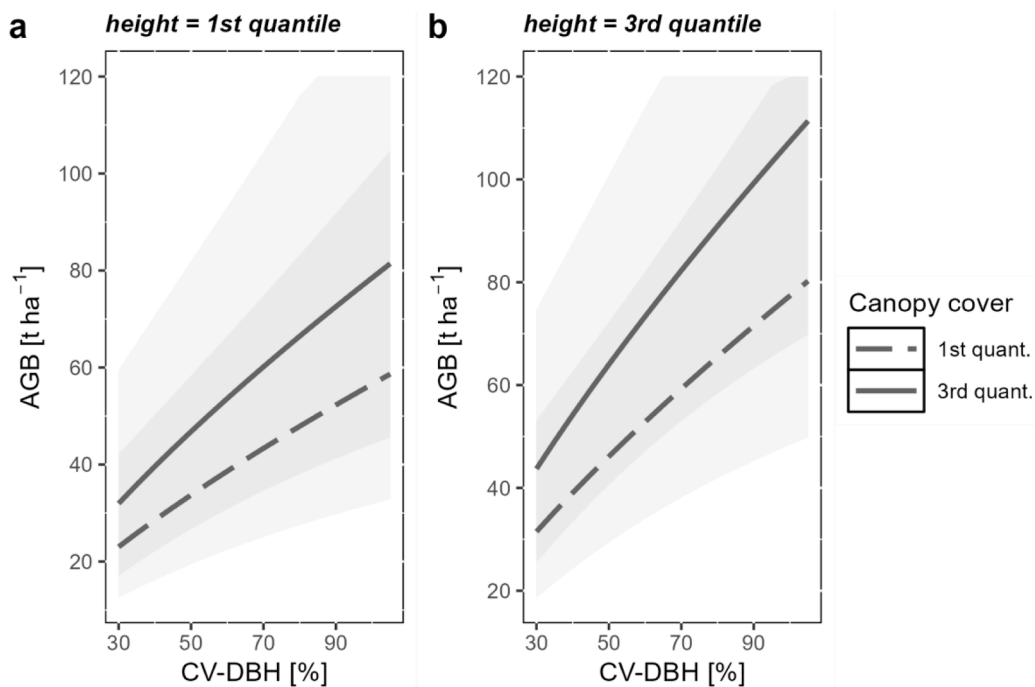
Our results showed that forest type was part of all finally selected



**Fig. 3.** Variable specific model predictions for different forest types with compact letter displays of post hoc test results. Letter displays of forest variables having no other final model parameter than forest type, are not shown. Colours signify different forest types same as in Fig. 2: red = Mopane Woodland, orange = Lowveld Woodland, yellow = Ironwood Forest, green = Mountain Woodland dry, light blue = Mountain Woodland moist, blue = Mistbelt Forest). Variables include A (tree density,  $k = \text{thousand}$ ), B (pole density,  $k = \text{thousand}$ ), C (mean height), D (above-ground biomass), E (deadwood volume), F (multi-stem tree ratio), G (coefficient of variation DBH), H (regeneration,  $k = \text{thousand}$ ), I (canopy cover), J (Shannon Index).



**Fig. 4.** Forest type specific model predictions for AGB depending on CV-DBH (coefficient of DBH variation). Solid, dashed and dot-dashed lines represent the 3rd quantile, the mean and the 1st quantile of the canopy cover respectively. The third model parameter mean height was set to forest type specific averages each. Predictions are only shown for CV-DBH ranges covered by data. Axis are logarithmized for reasons of better visualization. Gray buffers are the 95 % confidence interval for the predicted lines.



**Fig. 5.** AGB model predictions based on CV-DBH and different canopy cover ratios (1st quantile = dashed, 3rd quantile = solid) for: a (the 1st quantile of mean heights) and b (3rd quantile of mean heights). Gray buffers are the 95 % confidence interval for the predicted lines.

models and improved accuracy of model predictions compared to the models using water availability only (Q-II, Table 3). Together with the significant differences shown between the forest types (Fig. 3), this indicates that dendrometric and structural forest variables are driven not only by availability of water, but also by other factors influencing spatial distribution of forest types, like seed dispersal, species-specific survival and regeneration strategies, animal-plant interactions, genetic pool, nutrient supply, elevation, geology, aspect and fire proneness of the growth site (Geldenhuys, 2012).

On the one side, main species of the Mopane Woodland (*Colophospermum mopane*), and the Soutpansberg Mountain Woodland (*Pterocarpus angolensis*, *Pteleopsis myrtifolia*, *Pseudolachnostalis maprunefolia*, *Burkea Africana*, comp. Table S 9) show post fire regeneration strategies – e.g. fire induced dormancy release and re-sprouting after fire (Bellingham and Sparrow, 2000; Bond and Midgley, 2003; Syampungani et al., 2016). On the other side, dominant species of the Ironwood and the Mistbelt Forest are vulnerable to fire. Thus emerging only in lee side fire-shade areas and along gullies, or, in case of the Ironwood Forest,

mostly on rocky outcrops along mountain ridges where trees are protected by the natural barrier of rocky substrate (Geldenhuys, 1994; Geldenhuys and Tshaduli, 2023). Moreover, species like *Sclerocarya birrea* and *Parinari curatellifolia* occurring in the Lowveld and Soutpansberg Mountain Woodland, show endozoochoric (animal-digestion induced) seed dispersal and dormancy release (Helm et al., 2011; Kunz and Linsenmair, 2008; van Toor et al., 2019), thus depending on habitat specific mammal and bird populations (Mucina and Rutherford, 2006).

Also in terms of species variety the studied forest types did differ. While Mopane Woodland and Ironwood Forest are almost pure stands dominated by *Colophospermum mopane* and *Androstachys johnsonii* respectively; Lowveld Woodland, Soutpansberg Mountain Woodland and Mistbelt Forest have a strong variety of species, thus allowing for a broad range of different dendrometric and structural attributes to occur. Our model results for mean height (Fig. 3C) revealed that the four woodland types showed constant values, whereas Mistbelt Forest exceeded them by an order of magnitude. On the one hand this could be explained by lower canopy tree densities combined with less light competition leading to a stagnation of height growth in the woodlands. On the other hand, this could be the result of the moist microclimate and the location in fire shadow areas, as well as a different history and composition of their species pools. While most of the woodland species belong to the Zambezi centre of endemism (Assédé et al., 2020), the Mistbelt Forest belonging to the Afromontane Mountain Forests, is rather an archipelago-like remnant of the vegetation (White, 1981) that used to be there before climate got more arid and fires more frequent (in the late Neogene approx. 23 - 2.5 million years ago) caused by renewed geological uplifts of the Great Escarpment dividing moist coastal belts from more dry interior (Geldenhuys, 2012; Mucina and Rutherford, 2006). As a result of this forests turned into woodlands except of elevated sites with a special microclimate, today still being the refuge of these old species associations (Assédé et al., 2020). This could also be the reason for higher Mistbelt Forest values in terms of AGB, CV-DBH and regeneration compared to other forest types occurring in the Soutpansberg.

Our results also give insights into different regeneration dynamics among the studied forest types. The high canopy cover together with a high regeneration number in the Mistbelt Forest and the moist Mountain Woodland, indicate a shade tolerant regeneration, whereas Ironwood Forest also having a high canopy cover but a low amount of regeneration, points toward a strongly light demanding regeneration which cannot establish itself inside the shady stands. In the Ironwood Forest, we also found a surprisingly high tree density, AGB and deadwood volume in relation to its less beneficial pedo-climatic site conditions. This could be enabled by the very deep roots of *Androstachys johnsonii* tapping water from deep down (Magalhães and Seifert, 2015). Its surprisingly high deadwood amount (especially standing deadwood) could be explained by strong self-thinning of the dense stands in combination with a very high mechanical root stability and wood density leading to a very slow decay, but might be also the result of mass die-off during recent drought years in Limpopo (in 2002/03, 2013/14, 2014/15 and 2015/16) (Matimolane et al., 2024). Investigating ecological dynamics and reasons for the outstanding results of the Ironwood Forest could be aim of prospective studies.

#### 4.3. Influence of forest structure on forest AGB (Q-III)

Focussing on the dendrometric variable AGB, the results revealed that this ecologically important variable does not only change based on forest type and environmental variables like site-available soil water, but is also a function of internal structural variables. Our results showed that the structural variables canopy cover and CV-DBH, both were part of the finally selected model and, together with the dendrometric variable mean height, had a significant and substantial influence on AGB (Q-III, Fig. 4, Table S 7), thus improving the prediction of AGB (Table S 8). This is in line with the niche complementarity hypothesis, assuming

forests, diverse in species composition and structure can optimally use the available above and belowground resources, because of their range of different functional traits (Day et al., 2014; Mensah et al., 2018; Poorter et al., 2015). However, similar to other studies investigating drivers of AGB in African forests and woodlands (Atsri et al., 2020; Balima et al., 2021; Shirima et al., 2015), our study found a significant positive effect only for CV-DBH, as well as canopy cover but not for species diversity. A possible explanation for this could be that the effect of species diversity is already mainly manifested by structural diversity (Godlee et al., 2021; Mensah et al., 2023), which is supported by a correlation coefficient of 0.7 between species diversity and CV-DBH (Figure S 4). Our findings also provided evidence that the positive effect of CV-DBH on AGB increases with mean height (Fig. 5). We assume that this is due to the potential of stands with a taller mean height, to occupy more space, with higher canopy packing and to diversify their canopy into several layers (Zhang et al., 2024), thus accommodating light demand of different size classes and tree species, therefore utilizing resources above and below ground more efficiently compared to short stands having space only for one canopy layer.

## 5. Conclusion

To our knowledge this is the first study investigating most important forest and woodland types occurring along a climatic gradient in the Soutpansberg region. However, this also comes along with limitations. On the one side only a reduced number of plots could be investigated, on the other side we could not control for the effects of geology, elevation and aspect. Plots were also not located in protected reserves, but in communal land and therefore influences from human and livestock could not be excluded completely. Nevertheless, this study provides a broad set of ecologically relevant dendrometric and structural stand characteristics. We found a positive influence of site-available soil water on almost all investigated forest variables. Among the drivers influencing site-available soil water (climate, soil, catchment topography), especially climate played an important role. Apart from the environmental conditions investigated, this study identifies a strong influence also of forest type, which can be explained by different species compositions, survival strategies and fire adaptations occurring along the climatic gradient. Structural heterogeneity was detected to have a positive effect on AGB especially in taller stands having enough space to form several canopy layers. Considering the negative effects of climate change on soil available water and the resulting severe shifts in species composition and biome, we postulate that the 21st century will be marked by reduced dendrometric and structural attributes of forests and woodlands in the Soutpansberg region. This could lead to reduced ecosystem functions & services provided to local communities. The published forest and woodland metrics from this study could be of use as input data for landscape level modelling studies in the Soutpansberg region, as well as for designing local management plans and implementing bio-economic strategies for rural development in the Vhembe district. However, in order to be able to determine sustainable harvesting cycles and to apply adequate thinning intensities and silvicultural methods, apart from modelling the climax development stage only, more information is needed also on the different growth and regeneration dynamics. Further studies therefore should focus on mean annual growth rates, as well as on disturbance and light requirements of regeneration for the most important tree species occurring along the studied climatic gradient.

## CRedit authorship contribution statement

**Martin A. Honold:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Torben Hilmer:** Writing – review & editing, Validation, Supervision, Methodology,

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### Declaration of competing interest

The authors declare no competing interest.

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### Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.tfp.2025.100945](https://doi.org/10.1016/j.tfp.2025.100945).

### Data availability

Original plot level data set and metadata information are provided in the Appendix.

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