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Quantifying unseen woody biomass and diversity in understorey trees and shrubs at the extremes of water availability in the Miombo ecoregion

Hermane Diesse[a,b,*], John L. Godlee[c,b], Nichola Knox[d,g,i], Jonathan Muledi[b,e], Leena Naftal[a], David Nkulu[e], Ben Nkomba[e], Gabriel Uusiku[a], Kyle Dexter[b,c,f,h], Vera De Cauwer[a,b]

[a] *Namibia University of Science and Technology, 13 Jackson Kaujeua Street, Windhoek, Namibia*
[b] *Socio-Ecological Observatory for Studying African Woodlands – SEOSAW Network, UK*
[c] *School of GeoSciences, University of Edinburgh, Edinburgh, EH9 3FF, UK*
[d] *Downforce Technologies, 7 Albert Buildings, 49 Queen Victoria Street, London, EC4N 4SA, UK*
[e] *Ecologie, Restauration Ecologique et Paysage, Faculté des Sciences Agronomiques, Route Kasapa BP 1825, Université de Lubumbashi, Congo*
[f] *Royal Botanic Garden Edinburgh, Edinburgh, EH3 5LR, UK*
[g] *School of Earth and Space Exploration, Arizona State University, Phoenix, AZ, 85287, USA*
[h] *Department of Life Sciences and Systems Biology, University of Torino, Torino, Italy*
[i] *College of Science and Engineering, Flinders University, Adelaide, SA, Australia*

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ABSTRACT

The Miombo ecoregion covers eastern and southern Africa, with variations in plant species composition, structure, and biomass across a broad precipitation gradient. Most studies of woody plant communities focus exclusively on larger overstorey trees (≥5 or ≥10 cm stem diameter), overlooking the contribution of small trees and shrubs in the understorey, which can comprise a significant portion of total biomass and diversity. Here, we evaluate the contribution of both large overstorey and small understorey woody plants to species diversity and above-ground biomass (AGB), with 17 plots (0.5–1 ha) across five sites representing both extremes of rainfall gradient spanning the Miombo ecoregion, in northeast Namibia (500–700 mm mean annual precipitation, MAP) and southern Democratic Republic of Congo (DRC) (>1,200 mm MAP).

Mean AGB per site ranged from 21 to 119 Mg·ha^{-1}, increasing with rainfall, while the proportional AGB contribution of small trees, saplings, and shrubs decreased. In dry Namibia, small trees, saplings, and shrubs (<5 cm DBH) contributed up to 28.2% of total AGB (mean ± standard deviation: 18.3% ± 3.4%), whereas in wet DRC, they contributed only up to 2.5% (2.3% ± 1.4%).

Namibian sites, on average, contained a large proportion of woody species diversity exclusively in small trees and shrubs (<5 cm DBH), with 55 species representing 59.4% of the total diversity. In contrast, DRC sites had higher overall small woody plant diversity (66 species) but fewer species found exclusively as small individuals (25.2%), with many saplings that grow to larger trees. Understorey composition also differed, with saplings of overstorey trees dominating in DRC, while shrubs dominated in Namibia.

Our findings show that woody biomass and diversity in dry woodlands are substantially underestimated when studies focus only on larger trees. This highlights the need to consider all woody vegetation to better understand woody plant diversity and biomass variation.

1. Introduction

The Miombo ecoregion, spanning 11 countries in eastern and southern Africa, encompasses a variety of vegetation types, including the core Miombo woodlands dominated by the legume genera *Brachystegia*, *Julbernardia* and *Isoberlinia*, as well as other woodland types such as Mopane, Burkea-Terminalia, and Baikiaea woodlands (Timberlake and Chidumayo, 2011). These ecosystems provide numerous goods and services, including biodiversity conservation, carbon sequestration, and support for the livelihoods of millions of people (Ryan et al., 2016).

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* Corresponding author. Namibia University of Science and Technology, 13 Jackson Kaujeua Street, Windhoek, Namibia.
E-mail address: diessehermane@gmail.com (H. Diesse).

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Across the Miombo ecoregion, precipitation is a critical factor influencing ecosystem structure and function, resulting in highly heterogeneous vegetation patterns (Campbell, 1996; Godlee et al., 2021; Kuyah et al., 2016). Miombo woodlands *sensu lato*, found in regions with mean annual precipitation (MAP) between 600 and 1,400 mm, are characterised by an open tree canopy overstorey, a discontinuous understorey of shrubs and small trees, and a grass-dominated ground layer (Frost, 1996; Mayaux et al., 2004; Ryan et al., 2012). Canopy cover in these woodlands ranges from 20% to almost 100%, leading to varied understorey light conditions (Timberlake and Chidumayo, 2011). The canopy cover and diversity of large canopy trees generally increase with water availability (Godlee et al., 2021; Sankaran et al., 2005), illustrating the important role of precipitation. However, these patterns may not reflect those of small woody plants in the understorey which may exhibit different or even contrasting responses to environmental gradients due to an overriding influence of large canopy trees. Exceptions also exist, particularly in wetter regions, where local disturbances such as tree mortality or selective logging can create canopy gaps, allowing more light to reach the ground, and supporting a diverse understorey layer. While most studies assessing woody diversity and biomass stocks focus only on large overstorey trees (diameter at breast height ≥5 or 10 cm), research integrating all structural layers and growth forms is essential for a more complete understanding of ecosystems.

Woodland ecosystems comprise distinct vertical structural layers and their balance is strongly influenced by environmental factors, including precipitation. The overstorey layer, composed of larger trees, plays a crucial role in forest structure, diversity, and functioning (Ali et al., 2019; Balandier et al., 2022; Godlee et al., 2024). Overstorey trees, with their large canopies and root systems, influence the establishment and growth of the understorey layer through competition for water, soil nutrients, space, and light (Ahmad et al., 2019; Balandier et al., 2022). In wetter regions, such as the Miombo woodlands of the Democratic Republic of the Congo (DRC), higher rainfall promotes overstorey tree growth, leading to denser canopies that limit light penetration and reduce the understorey layer contribution to the total above-ground biomass (AGB) stocks (Frost, 1996; Munalula et al., 2020; Sankaran et al., 2005). This relationship, however, also extends to understorey biodiversity. Increased canopy cover and tree density favour shade-tolerant species while restricting the establishment of light-demanding species (Baker et al., 2020; Dormann et al., 2020). In contrast, drier regions like Namibia's woodlands have more open canopies due to lower precipitation, allowing greater light availability for the understorey layer and potentially higher understorey biomass and woody plant species (Fig. 1). Therefore, in dry woodlands, the understorey layer may constitute a major contribution to overall biomass stocks and woody plant diversity. Although some studies of wet forests have suggested that stand-level AGB can be predicted from a few large-sized trees (Ali et al., 2019; Slik et al., 2013), this view may overlook the significant roles of small trees and shrubs, especially in more open woodlands in lower rainfall areas, which can hold a substantial and diverse understorey component (Sagar et al., 2008).

Smaller woody plants in the understorey layer are not frequently included in assessments of woody plant diversity and AGB monitoring (Huff et al., 2018). The minimum diameter at breast height (DBH) is commonly 10 cm in wet tropical forest biomass and diversity studies (Chave et al., 2014) and commonly 5 cm in dry tropical woodlands (Moonlight et al., 2020; SEOSAW partnership, 2021). Including smaller understorey woody plants in field inventories can be time-consuming due to their abundance and are perceived to contribute little to total AGB stocks and species diversity (Kindermann et al., 2022; Le et al., 2018). Yet, many studies have shown the critical role played by the understorey layer in determining fire behaviour, provision of non-timber products and firewood, soil protection, carbon sequestration, overstorey regeneration (Ferrara et al., 2023; Lombaerde et al., 2018; Suchar and Crookston, 2010), and biodiversity (Bricca et al., 2023). A high proportion of small trees in the understorey suggests good recruitment of tree species while a lack of small trees suggests potential future changes to stand structure and function (Muvengwi et al., 2020). Areas with dense and diversified understorey vegetation increase wildlife species presence by providing them with palatable forage and fruit which can help with the dispersal of trees and thus habitat stability (Lone et al., 2014; Nijland et al., 2014).

Investigating the diversity and contribution to the total biomass of smaller understorey woody plants in the Miombo ecoregion is imperative for understanding the full extent of forest functionality and guiding sustainable management efforts (Návar et al., 2004). Integrating

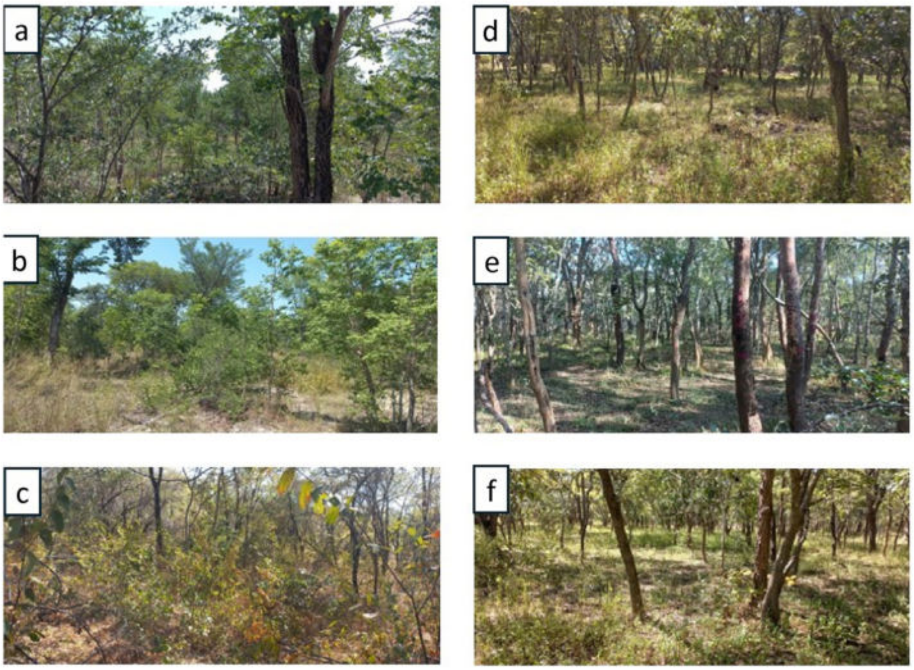

Fig. 1. Typical representation of the understorey layer in dry and wet Miombo. (**a**), (**b**) and (**c**) are respectively SK1, H3 and Z1. (**d**), (**e**) and (**f**) are respectively M2, M1 and M3. These pictures illustrate how dense is the understorey layer in dry Miombo compared to wet Miombo.

understorey assessments can reveal their significant role in contributing to above-ground biomass (AGB) and enhance our understanding of ecosystem diversity (Le et al., 2018). This improved understanding would enable a reassessment of ecosystem service values and lead to more informed conservation priorities and targeted policies, such as the United Nations' Reducing Emissions from Deforestation and Forest Degradation Plus (REDD+). Despite its ecological importance, however, there remains a notable knowledge gap concerning the composition and biomass stocks of the understorey layer within the Miombo ecoregion.

This study describes covariation in woody species diversity and AGB in larger overstorey trees and understorey woody plants across the dry woodlands of Namibia and the wet Miombo woodlands of DRC, which represent the extremes of water availability in the Miombo ecoregion. Most previous research in the Miombo ecoregion on ecosystem structure has been carried out at single sites which precludes studying the role of variation in important environmental factors such as rainfall and water availability. Thus, there is a need to incorporate data on a large scale to better understand the composition, structure, and functioning of the Miombo ecoregion (Muvengwi et al., 2020). This study represents the first effort to detail the contribution of overstorey and understorey trees and shrubs to species diversity, woodland structure, and woody biomass in five sites located in two areas within the Miombo ecoregion, representing an extreme contrast in rainfall and water availability. We hypothesise that the understorey in drier Namibian woodlands will make a substantial (>10%) contribution to woody biomass stocks and plant species richness, while their contribution will be significant (>2%) but more limited in wetter woodlands (in the DRC).

2. Materials and methods

2.1. Study area

Data were collected in five sites located in two areas, representing extremes of the rainfall gradient observed across the broader Miombo ecoregion (Fig. 2) (Burke, 2002; Timberlake and Chidumayo, 2011). The dry woodlands of Namibia, situated in the northeastern part of the country, are mainly composed of Mopane woodlands (dominated by *Colophospermum mopane*) and open *Burkea*, *Pterocarpus*, and *Terminalia* woodlands (De Cauwer, 2023; Strohbach and Petersen, 2007). The woodlands of the DRC receive higher and more evenly distributed precipitation, resulting in higher water availability throughout the year. The vegetation is typical Miombo woodland, dominated by trees belonging to the legume genera of *Brachystegia*, *Julbernardia*, and *Isoberlinia* (Campbell, 1996).

The three Namibian study sites fall within the Kavango East Region (Hamoye State Forest), Otjozondjupa Region (Kanovlei State Forest) and Zambezi Region (Zambezi State Forest). Most of the soils in the northeastern part of Namibia are poor arenosols and have low water retention capacity (Hengl et al., 2014). The MAP in Hamoye is 560 mm whereas the MAP in Kanovlei is 500–550 mm (Atlas of Namibia Team, 2022; Cauwer et al., 2016; Mayr et al., 2018). The Zambezi region has the highest rainfall in Namibia with MAP between 600 and 700 mm (Mendelsohn et al., 2002), occurring mainly from November to March (Burke, 2006). The plots in the Zambezi State Forest were set up in the Sachinga Livestock Development Centre, a government farm under the Ministry of Agriculture Water and Land Reform. Wildfires impact the whole region, with limited controlled burning management implemented, the Sachinga site however has been actively protected from fire disturbance and fuelwood removal.

The two field sites in the DRC are in the Mikembo Reserve and Kibundu Village, both situated in the Upper Katanga Province in the southeastern part of the country. Mean annual temperature (MAT) is 20 °C, and MAP is 1,200 mm, occurring mainly during the rainy season from November to April (Malaisse, 1997; Muledi et al., 2016). The soils of the Miombo woodlands in Upper Katanga are ferralsols, with a flat topography, but regularly punctuated (~3 per ha) by large termite mounds up to 8 m in height (Muledi et al., 2016). Established in 2003, the Mikembo reserve is protected from fire disturbances and fuel-wood

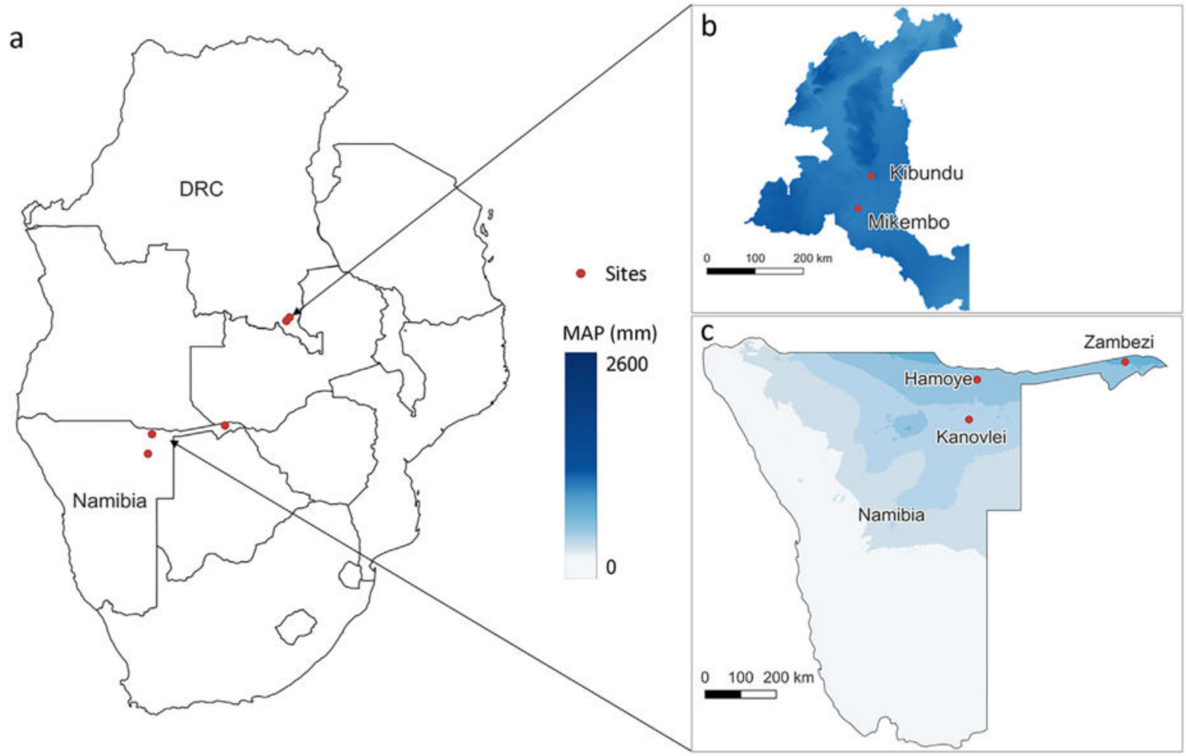

Fig. 2. Location of study sites within southern Africa. **(a)** Upper Katanga Province in the Democratic Republic of Congo (DRC) **(b)**, and Namibia **(c)**. Panels b and c are shaded by Mean Annual Precipitation (MAP, mm). Kanovlei = 500–550 mm MAP; Hamoye = 560 mm MAP; Zambezi = 600–700 mm MAP; Kibundu = 1,200 mm MAP; Mikembo = 1,200 mm MAP.

cutting (Muledi et al., 2016). In contrast, Kibundu Village, a community forest, has experienced disturbances from fire and fuel-wood harvesting. However, it was placed under protection in 2022, limiting any subsequent wood harvesting.

2.2. Data collection

All data were collected in 2023 during the period of peak vegetation cover. A total of 17 plots were established across the five sites, comprising seven plots of 1 ha and 10 plots of 0.5 ha. Variations in plot size accounted for differences in vegetation structure while balancing logistical constraints, ensuring a representative sample of biomass and species diversity across the study sites (Table S1). Overstorey vegetation was measured for the entire plot following the SEOSAW protocol v3.6 (https://seosaw.github.io/manuals.html).

Overstorey vegetation comprising large trees was defined as tree stems with a diameter at breast height (DBH, 1.3 m above ground) ≥ 5 cm. For each overstorey stem the following data were recorded: name of species, DBH at 1.3 m (or higher in case of possible deformities), crown diameter in two perpendicular directions, and stem height. Overstorey trees were measured across the entire 0.5/1 ha plot.

Understorey vegetation comprising small trees and shrubs was defined as woody individuals with stem diameter <5 cm and with a plant height >50 cm. Understorey vegetation was measured within nested plots of 25 m × 25 m within each 0.5/1 ha plot. A total of five subplots were established in each 1-ha plot while two subplots were established in each 0.5-ha plot (Fig. 3). The following attributes were measured for the understorey woody vegetation: name of species, stem diameter measured with a Vernier calliper between 0.1 and 0.3 cm height above the ground, crown diameter in two perpendicular directions, height (measured by using a Vertex laser rangefinder or a measuring stick), and status, including dead and resprouting stems. All individuals were identified to the species level, except for two species comprising 42 individuals (3.6%) in the Zambezi State Forest, which were only identified by local names. Additionally, three species were assigned family-level morphospecies identities.

2.3. Data analysis

Woody plant density was calculated at the subplot level for all plots except for those in the Kibundu site, where the calculation was done at the plot level (0.5 ha) due to a lack of tree location data. To maintain consistency across sites, we extrapolated woody plant density to a 1-ha scale in all cases, regardless of whether measurements were taken at the subplot or plot level, ensuring comparability of woody plant density estimates across all sites.

To ensure consistency for diversity comparisons, 1-ha plots were divided into two halves, resulting in a 0.5-ha size for the overstorey diversity analysis. For understorey diversity analysis, two subplots per 0.5 ha were consolidated into one. In total, we analysed 24 plots of 0.5 ha for the overstorey diversity and 24 subplots of 0.125 ha total for the understorey diversity. All diversity metrics were calculated for both overstorey and understorey using the vegan package in R (Oksanen et al., 2015). We calculated the Shannon-Wiener index (H') using: $H' = \sum_{i=1}^{s} p_i \ln p_i$, where p_i is the proportion of individuals of species i, and ln is the natural logarithm. The value of H' ranges from 0 to $H'_{\max}$ which depends on the species richness. Secondly, we estimated species abundance evenness represented by the Shannon equitability index (J) (Smith and Wilson, 1996) using: $J = \frac{H'}{\ln s}$, where s is the species richness, calculated as the sum of species from each subplot. The evenness index measures how similar are the abundances of the different species within a community. A higher index value indicates a more balanced abundance of species, meaning that a few species do not dominate the community.

AGB of large trees in the overstorey layer was calculated using equation 4 from Chave et al. (2014) based on DBH, species woody density, and height. Height measurements were collected for all trees at the Hamoye, Mikembo, and Kibundu sites, as well as the K1 and SK2 plots at the Kanovlei site. However, in the Zambezi site and the SK1 plot in Kanovlei, height measurements were limited to selected trees within the plots. For trees without height measurements, heights were predicted using the Regional Generalized Height Model developed by Mugasha et al. (2019), which has a percentage Root Mean Square Error of 31%, and uses mean annual precipitation, basal area per hectare and DBH as explanatory variables.

To estimate understorey AGB, we used the models developed by Conti et al. (2019). These models have previously been applied to Miombo woodlands, including in the Zambezi State Forest by Kindermann et al. (2022). For multi-stemmed shrubs we used the canopy-based models, with two predictors including height (H) and mean crown diameter (CD) (Conti model equation 4). For single-stemmed trees, we used equation 2 and equation 3, which incorporate basal diameter (BD) and either CD or H. After calculating the AGB of individual woody plants, we determined each plot's total AGB per hectare by summing individual AGB values and dividing by the plot area. A diameter threshold of 10 cm DBH is

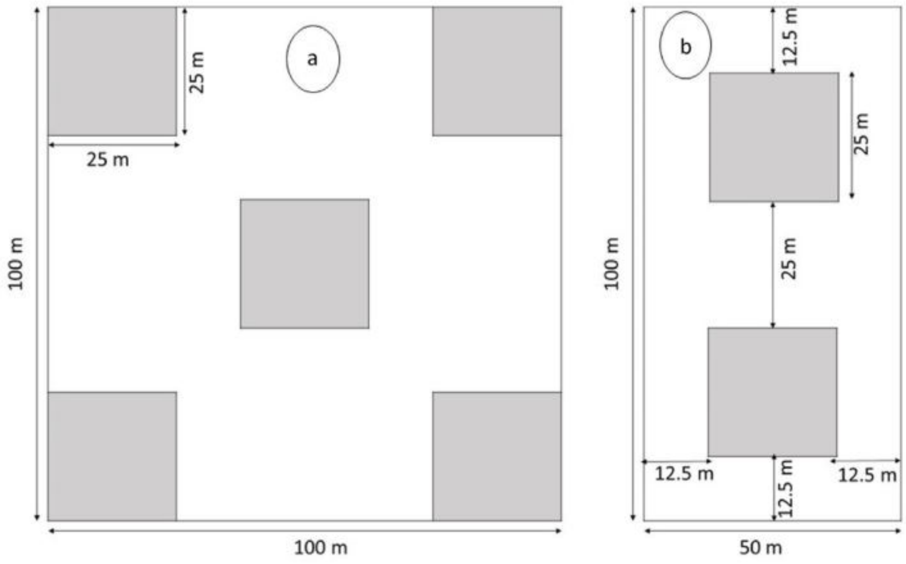

Fig. 3. Plot design of the understorey subplots; **a** = five nested plots within 1-ha or **b** = two nested plots within 0.5-ha.

sometimes used to define overstorey trees in tropical forest plots (e.g. RAINFOR, https://rainfor.org/). To assess the sensitivity of our findings to the DBH threshold, we recalculated the contribution of the understorey to total AGB by increasing the threshold to 10 cm DBH. We calculated the basal area of each stem (g_i) for the overstorey layer using: $g_i = \pi(d_i/2)^2$, where d_i is the stem diameter of stem i recorded at 1.3 m. Each plot's basal area per hectare was calculated as the sum of overstorey tree stem basal areas divided by plot area (Table S1).

Understorey plants were categorized as either trees or shrubs based on field observations and descriptions from Mannheimer and Curtis (2018) and Van Wyk and Van Wyk (2013). Understorey trees were further differentiated into saplings or small trees according to their growth potential. Saplings are juvenile individuals of species that can eventually grow to large overstorey trees, while small trees are defined as individuals that remain confined to the understorey throughout their life cycle. A species was classified as a small tree if more than 90% of individuals were found in the understorey layer. This threshold was chosen based on empirical testing of various percentages (80%, 85%, 90%, and 95%). The 90% criterion effectively distinguishes species that are predominantly restricted to the understorey while minimizing misclassifications of saplings that may occasionally appear in the overstorey.

For diversity analyses, growth forms were grouped into ‘small trees and shrubs’, representing plants that remain in the understorey layer, and ‘saplings and large trees’, representing the plants that can reach the overstorey. For biomass stock analyses, growth forms were grouped into ‘small trees, shrubs and saplings’ i.e. the understorey, and ‘large trees’ i.e. the overstorey. These two different groupings both aimed to evaluate the diversity and biomass that may be respectively overlooked when focusing solely on trees with a diameter at breast height (DBH) $\geq$ 5 cm.

2.4. Statistical analysis

Statistical analysis was performed using R software (R Core Team, 2023). We checked the assumptions of parametric analysis for all data.

Linear Mixed effects models (LME) were employed to evaluate the relationships between overstorey and understorey characteristics, while accounting for potential variability across sites. The first set of LME assessed the influence of overstorey basal area on understorey species richness. Separate models were developed for understorey tree species richness and understorey shrub species richness with overstorey basal area included as a fixed effect and site as a random intercept term to account for unmeasured variability among sites.

The second set of LME assessed the influence of the overstorey basal area on the percentage of total AGB stored in the understorey layer. Overstorey basal area was included as a fixed effect and site again was treated as a random intercept term effect.

Prior to modelling, all continuous variables were centred and standardized using the scale function in R to make the model results reliable and easier to interpret. LME models were implemented using the lme4 package (Bates et al., 2015), and model diagnostics (e.g., linearity, homoscedasticity, and residual normality) were assessed using the performance package (Lüdecke et al., 2021) (Figs. S1–S3, Tables S3 and S4).

A Kruskal-Wallis test, followed by a Dunn's test (using the Bonferroni method) was applied to compare the species richness, J and H' among sites because the assumptions required for parametric tests were not met.

A chi-squared test was performed to assess whether the different growth forms composing the understorey layer (small trees and saplings in one part and shrubs in another) have similar proportions of individuals at the study sites.

To analyse plant height structure, a total of eight classes were created (0.5–1, 1–2, 2–3, 3–4, 4–5, 5–7.5, 7.5–10 m and above 10 m).

A Mann-Whitney test was used to compare H' and the AGB stored in different understorey growth forms (shrubs, small trees, saplings).

3. Results

3.1. Floristic composition of the understorey and overstorey layers

Across all plots, 7,922 individuals were documented in the understorey layer and 5,118 individuals in the overstorey layer. Overall, the understorey layer in DRC sites had 67 species belonging to 50 genera and 27 families while the understorey layer in Namibian sites had 55 species belonging to 35 genera and 15 families. Overall, the overstorey layer in DRC sites had 79 species belonging to 54 genera and 27 families, whereas Namibian sites had 34 species belonging to 24 genera and 12 families. Examining family level composition, we found Fabaceae to be dominant across all layers in both the DRC and Namibia comprising 30 (40%) and 19 (28%) species respectively in the overstorey and understorey layers in DRC and 12 (38%) and 16 (30%) species in the overstorey and understorey in Namibia.

Analysis of plant growth forms in the understorey layer revealed significant differences across sites ($\chi^2 = 1630.7$, df = 4, p-value < 0.001). In the DRC, small trees constituted 15.4% of plants sampled in the understorey, shrubs constituted 11.4%, and saplings of large trees constituted 74.5%. In contrast, in Namibia, small trees constituted 12%, shrubs constituted 47.3%, and saplings of large trees constituted 40.6%.

In Namibia, the understorey was dominated by *Ochna pulchra* (16%), *Psydrax livida* (11%), *Baphia massaiensis* (10%), while in the overstorey, *Burkea africana* (24%), *Combretum collinum* (12%), *Dialium engleranum* (12%) were the most abundant. In the DRC, the understorey was dominated by *Triumfetta dekindtiana* (15%), *Bridelia duvigneaudii* (13%), and *Julbernardia globiflora* (10%), while in the overstorey, *Julbernardia paniculata* (17%), *Brachystegia boehmii* (13%), and *Diplorhynchus condylocarpon* (9%) were the most dominant.

3.2. Distribution of species diversity and woody density across forest layers

Total woody plant species richness (including the understorey and overstorey) ranged from 18 to 53 species per 0.5 ha. In general, species diversity and woody plant density increase along the rainfall gradient. A post-hoc Dunn's test following the Kruskal-Wallis analysis revealed significant differences in the Shannon-Wiener index (H') among sites ($\chi^2 = 17.072$, df = 4, p-value < 0.01), with Kibundu having significantly higher H' than Hamoye and Kanovlei (Fig. 4). Additionally, a post hoc Dunn's test following the Kruskal-Wallis analysis revealed significant differences in Shannon equitability (J) across sites ($\chi^2 = 14.52$, df = 4, p-value < 0.01) with Kibundu having significantly higher J than Mikembo and Hamoye.

Focusing on the overstorey layer, species diversity was significantly ($\chi^2 = 12.638$, df = 1, p-value < 0.01) higher in the DRC sites compared to the Namibian sites (Fig. 4). A post-hoc Dunn's test following the Kruskal-Wallis analysis revealed that overstorey species richness at Kanovlei was significantly lower than at Kibundu and Mikembo (Table 1). Additionally, the Shannon-Wiener index (H') at Kanovlei was significantly lower than at Kibundu and Mikembo, while Kibundu had a higher H' than Hamoye ($F = 11.52$, $p < 0.01$). Shannon equitability (J) for the overstorey also varied significantly among sites, with Kibundu showing a higher J than Mikembo ($F = 3.18$, $p < 0.05$).

Similarly, in the understorey layer, species diversity indices were significantly higher in the DRC sites compared to the Namibian sites (Fig. 4). A post-hoc Dunn's test following the Kruskal-Wallis analysis revealed that understorey species richness at Kanovlei was significantly lower than at Mikembo and Zambezi. In contrast, Kibundu's understorey species richness was significantly lower than that at Mikembo and Zambezi. However, no significant differences in H' and J were detected for the understorey layer across the sites.

Except in Zambezi, shrubs consistently exhibited the lowest H' and

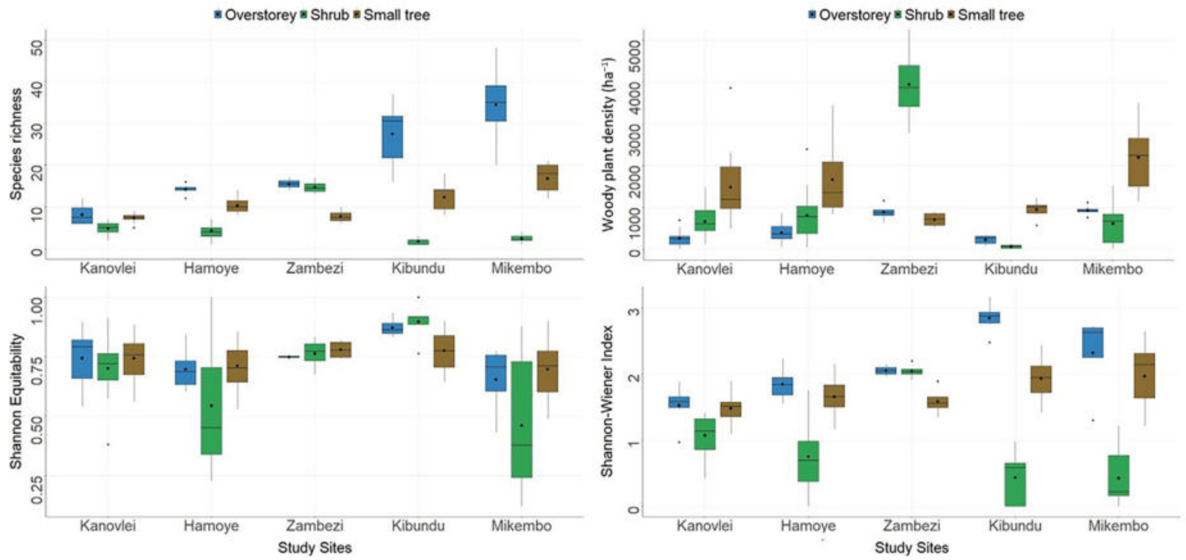

Fig. 4. Variation in species richness, Shannon Equitability, woody plant density, and Shannon-Wiener index by site for understorey (small trees and shrubs) and overstorey (large trees and saplings) layers. Sites are ordered by mean annual precipitation: Kanovlei = 500–550 mm; Hamoye = 560 mm; Zambezi = 600–700 mm; Kibundu = 1,200 mm; Mikembo = 1,200 mm.

Table 1

Comparison of species richness, Shannon-Wiener index, Shannon equitability index, above-ground biomass (AGB), and woody plant density between overstorey and understorey layers. Values are presented as mean ± standard deviation. Letters indicate significant differences among sites for each metric within each layer (overstorey or understorey), with different letters (e.g., a, b, c) denoting statistically distinct groups ($p < 0.05$).

Overstorey layer						
Country	Site	Species richness	Shannon-Wiener	Shannon equitability	AGB (Mg·ha^{-1})	Woody plant density (ha^{-1})
Namibia	Kanovlei	8.1 ± 2.5 a	1.5 ± 0.3 a	0.74 ± 0.13 ab	15.4 ± 4.1 a	228 ± 145 a
Namibia	Hamoye	14.1 ± 1.3 ab	1.8 ± 0.2 ac	0.70 ± 0.09 ab	26.4 ± 9.4 a	364 ± 158 ac
Namibia	Zambezi	15.5 ± 2.1 ab	2.1 ± 0.1 ab	0.75 ± 0.01 ab	58.3 ± 0.0 ab	829 ± 168 ac
DRC	Kibundu	27.5 ± 8.1 b	2.8 ± 0.2 b	0.87 ± 0.04 b	51.0 ± 20.4 ab	233 ± 113 a
DRC	Mikembo	34.5 ± 11.4 b	2.3 ± 0.6 bc	0.66 ± 0.16 a	117.3 ± 43.2 b	901 ± 181 bc
Understorey layer						
Country	Site	Species richness	Shannon-Wiener	Shannon equitability	AGB (Mg·ha^{-1})	Woody plant density (ha^{-1})
Namibia	Kanovlei	15.5 ± 0.8 a	2.0 ± 0.1 a	0.75 ± 0.04 a	5.9 ± 3.1 a	2078 ± 504 ab
Namibia	Hamoye	20.3 ± 1.9 ab	2.0 ± 0.2 a	0.68 ± 0.06 a	4.2 ± 1.2 ac	2339 ± 580 b
Namibia	Zambezi	29.0 ± 2.8 ab	2.6 ± 0.1 a	0.77 ± 0.04 a	8.7 ± 1.5 a	5048 ± 996 b
DRC	Kibundu	19.0 ± 3.5 ac	2.2 ± 0.3 a	0.76 ± 0.09 a	1.2 ± 1.4 b	1027 ± 238 ab
DRC	Mikembo	34.0 ± 7.1 bc	2.3 ± 0.6 a	0.67 ± 0.15 a	1.8 ± 0.4 bc	2671 ± 872 a

species richness, with values decreasing as rainfall increased. A Mann-Whitney test revealed a significant difference ($W = 278$, $p < 0.001$) in the H' between shrubs and trees within the understorey layer across the sites. Specifically, trees consistently exhibited a higher H than shrubs, except in Zambezi.

Comparing small trees and shrubs with saplings and large trees, a Mann-Whitney test revealed significant differences between them in both H' ($W = 43$, $p < 0.001$) and J ($W = 160$, $p < 0.01$) across all sites (Fig. 5). Species richness, H', and J for saplings and large trees increased with rainfall. In contrast, species richness and H' for small trees and shrubs decreased with rainfall on average. No significant differences in J were observed for small trees and shrubs across the sites.

Exploring the influence of overstorey conditions on understorey species richness, LME revealed a significant positive effect ($\rho = 0.57$, $p < 0.001$) of overstorey basal area on understorey tree species richness (small trees and saplings). This finding indicates that a higher overstorey basal area is associated with a greater richness of small trees in the understorey layer. The variance due to site was 0.45, suggesting a moderate proportion of the variation in understorey tree species richness is explained by the site-specific effects. In contrast, no significant effect of overstorey basal area was observed on understorey shrub species richness ($\rho = -0.07$, $p > 0.05$) (Fig. 8). Although the relationship was not significant, the variance due to site was 1.82, suggesting that most of the variation in shrub species richness is explained by differences among sites. When excluding the Kibundu site, which is characterised by the highest levels of overstorey tree harvesting due to human activities, the relationship between understorey shrub species richness and overstorey basal area is more evident but remains statistically non-significant ($\rho = -0.42$, $p > 0.05$). An analysis of the proportion of species richness across structural layers and growth forms reveals distinct patterns influenced by rainfall gradients. In DRC, the percentage of saplings (juveniles of large trees) and large trees is higher (74.5%), with more species found exclusively in the overstorey, while in Namibia, the proportion of small trees and shrubs is higher (59.4%), decreasing with rainfall (Table 2).

The mean woody plant density of the plots located in Hamoye and Kanovlei followed a right-skewed distribution where the highest number of woody plant densities was found between 1 and 2 m and decreased with the height classes (Fig. 6). However, the plots located in Zambezi, Kibundu and Hamoye showed a second peak for trees between 5 and 7.5 m height. Focusing only on the overstorey trees, the mean height per plot ranged from 4.7 m in the drier site to 11.56 m in the wetter site.

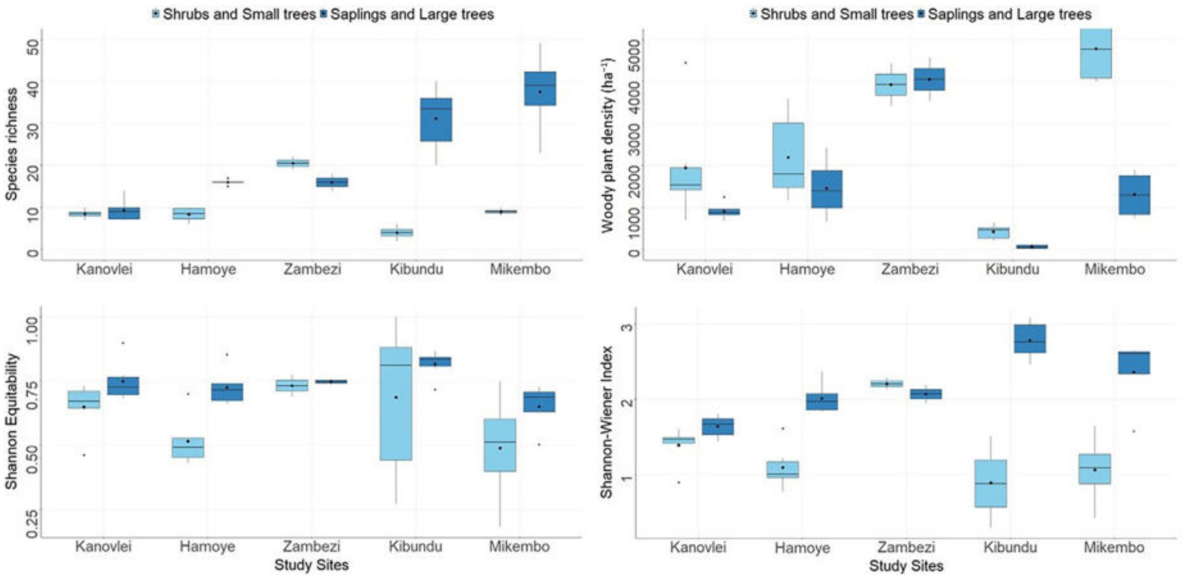

Fig. 5. Changes in diversity indices and woody plant density for shrubs and small trees vs. saplings and large trees. Sites are ordered by mean annual precipitation: Kanovlei = 500–550 mm; Hamoye = 560 mm; Zambezi = 600–700 mm; Kibundu = 1,200 mm; Mikembo = 1,200 mm.

Table 2
Species richness and percentage contribution to total species richness of small trees, shrubs, and saplings and large trees across sites.

Country	Site	Small trees	Shrubs	Saplings and large trees
Namibia	Kanovlei	2.67 ± 0.58 (13.31% ± 2.35%)	8.67 ± 0.58 (43.75% ± 5.62%)	8.67 ± 2.08 (42.94% ± 4.53%)
Namibia	Hamoye	1.67 ± 0.58 (6.68% ± 2.58%)	8.67 ± 2.31 (34.01% ± 7.94%)	15.00 ± 1.73 (59.31% ± 7.34%)
Namibia	Zambezi	4.00 ± 0 (13.57% ± 2.56%)	16.50 ± 2.12 (55.31% ± 3.36%)	9.50 ± 3.54 (31.1% ± 5.92%)
DRC	Kibundu	2.50 ± 0.84 (8.1% ± 3.64%)	1.80 ± 0.84 (5.46% ± 1.39%)	28.67 ± 7.31 (87.35% ± 4.43%)
DRC	Mikembo	5.67 ± 1.15 (13.1% ± 3.39%)	4.00 ± 1.00 (9.85% ± 5.5%)	35.33 ± 12.50 (77.05% ± 8.17%)

3.3. *Contribution of each layer to the total biomass*

The mean total AGB of each site ranged from 21 Mg·ha^{-1} in Kanovlei, Namibia to 119 Mg·ha^{-1} in Mikembo, DRC. AGB increased along the precipitation gradient. When analysing the distribution of AGB across height classes, we found that, more than 60% of AGB in Namibia was stored in plants taller than 5 m (Kanovlei = 63.5%; Hamoye = 78.9%; Zambezi = 85.7%). In contrast, in DRC, we found that more than 95% of AGB was stored in plants taller than 5 m (Kibundu = 95.1% and Mikembo = 98.1%) (Fig. 6).

Analysing the contribution of each layer to the total AGB, Fig. 7 shows that a large part of the AGB was stored by large trees in the overstorey (71.8% in Kanovlei, 85.1% in Hamoye, 87.8% in Zambezi, 97.5% in Kibundu and, 98.5% in Mikembo). The LME confirmed that an increase in overstorey basal area is associated with a significant reduction in the percentage of AGB stored in the understorey layer (Fig. 9; $\rho = -0.59$, $p < 0.05$).

When the DBH threshold for overstorey trees was increased to 10 cm, the contribution of the understorey layer to total AGB increased. Under

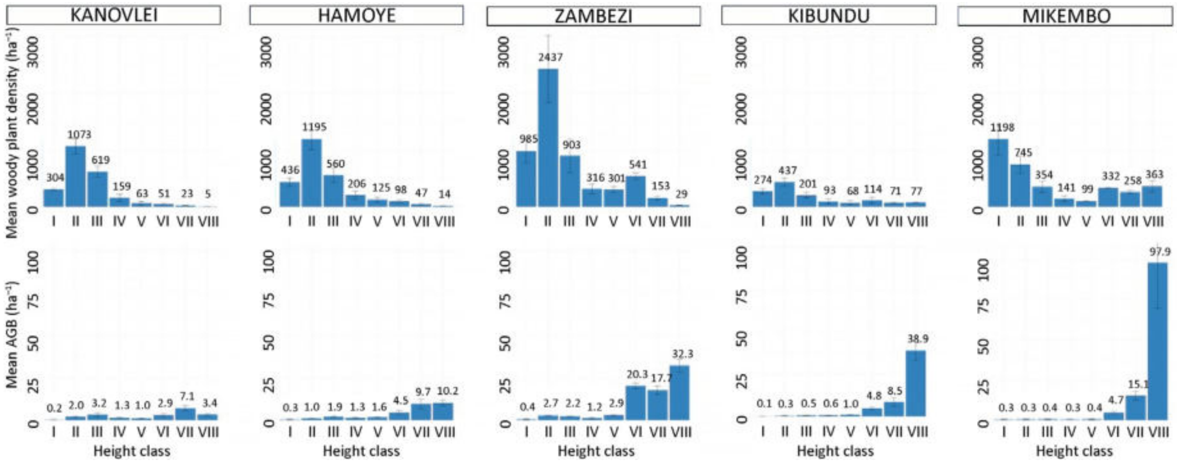

Fig. 6. Distribution of woody plant density (top row) and AGB across height classes (bottom row). I = 0.5–1 m height, II = 1–2 m height, III = 2–3 m height, IV = 3–4 m height, V = 4–5 m height, VI = 5–7.5 m height, VII = 7.5–10 m height, VIII ≥10 m height. Sites are ordered by mean annual precipitation: Kanovlei = 500–550 mm; Hamoye = 560 mm; Zambezi = 600–700 mm; Kibundu = 1,200 mm; Mikembo = 1,200 mm.

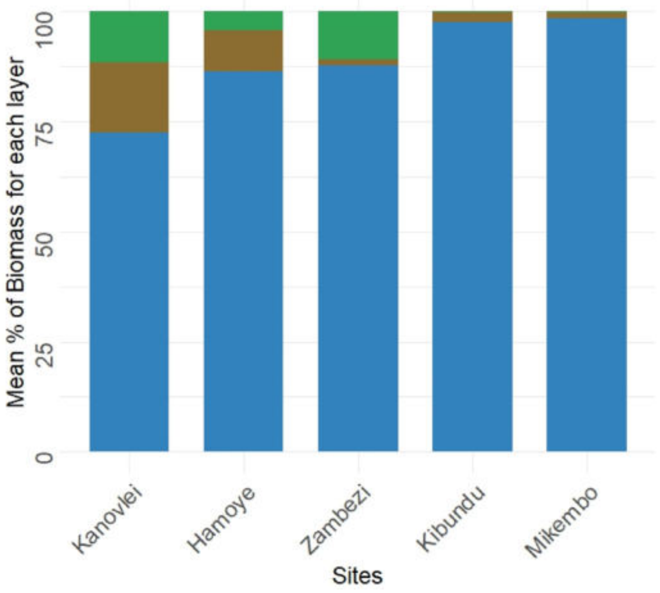

Fig. 7. Above-ground biomass (AGB) stored by each layer within each site with a threshold of DBH ≥5 cm. The green colour is for the shrubs, the brown colour is for the small trees and saplings growth form and the blue colour is for the overstorey trees Sites are ordered by mean annual precipitation: Kanovlei = 500–550 mm; Hamoye = 560 mm; Zambezi = 600–700 mm; Kibundu = 1,200 mm; Mikembo = 1,200 mm.

this threshold, the overstorey contributed 67.5% in Kanovlei, 80.8% in Hamoye, 76.4% in Zambezi, 93.1% in Mikembo, and 97.2% in Kibundu. These results illustrate that in drier woodlands, the understorey layer represents a considerable proportion of the total AGB, but its contribution decreases along the precipitation gradient.

We investigated the contribution of each species to the plot-level AGB (Table 3). We found that the top five species contributed to the plot-level overstorey AGB at 97% in Kanovlei, 91% in the Hamoye, 84% in Zambezi, 64% in Kibundu, and, 66% in the Mikembo. This trend reflects an increase in diversity along the rainfall gradient. For the understorey layer, the top five species contributed to the plot-level understorey AGB as follows: 80% in the Kanovlei, 64% in the Hamoye, 60% in the Zambezi, 65% in Kibundu, and, 67% in Mikembo.

4. Discussion

4.1. Variation in AGB across layers and rainfall gradient

Our findings demonstrate that biomass studies in dry woodlands that only consider woody biomass from large trees, defined by thresholds of ≥5 cm or ≥10 cm DBH, underestimate total woody biomass by an average of 18.3% and 24.1%, respectively. Understorey biomass contribution decreases with increasing rainfall. The estimated percentage of total AGB stored in the understorey layer in dry woodlands in the Miombo ecoregion aligns with the findings of a few previous studies on understorey biomass (Colgan et al., 2013; Frost, 1996; Kindermann et al., 2022). For instance, Kindermann et al. (2022), reported that the shrub

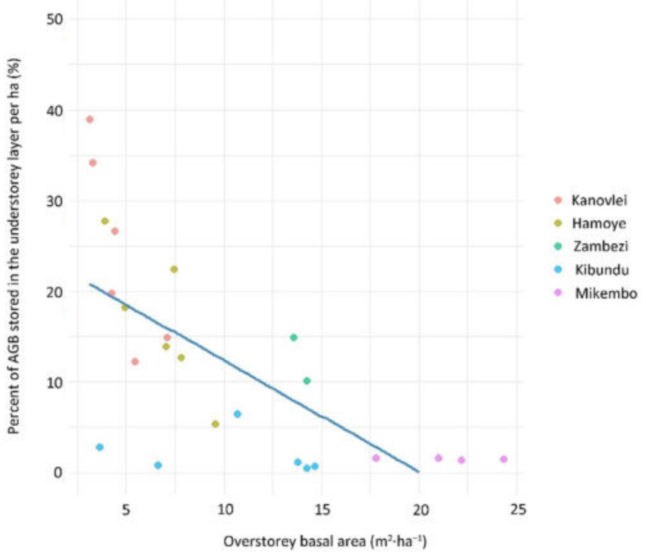

Fig. 9. Variation of the percentage of the AGB stored in the understorey layer with the overstorey basal area. The blue line represents the linear mixed model fit by REML. Sites vary in mean annual precipitation: Kanovlei = 500–550 mm; Hamoye = 560 mm; Zambezi = 600–700 mm; Kibundu = 1,200 mm; Mikembo = 1,200 mm.

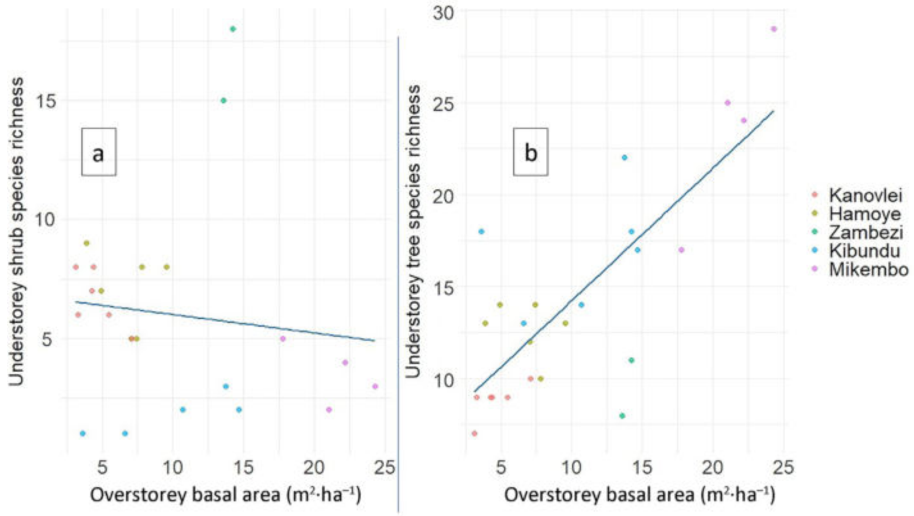

Fig. 8. Variation of understorey species richness (**a** = understorey shrub species richness and **b** = understorey tree species richness) with overstorey basal area. The blue lines represent the linear mixed model fit by REML. Sites vary in mean annual precipitation: Kanovlei = 500–550 mm; Hamoye = 560 mm; Zambezi = 600–700 mm; Kibundu = 1,200 mm; Mikembo = 1,200 mm.

Table 3
Top five species contributing to overstorey and understorey above-ground biomass (AGB) at each site.

Site	Overstorey			Understorey		
	Species	Mean AGB (Mg·ha^{-1})	Mean woody plant density (ha^{-1})	Species	Mean AGB (Mg·ha^{-1})	Mean woody plant density (ha^{-1})
Hamoye	*Baikiaea plurijuga*	6.71	17	*Dialium engleranum*	1.05	239
	Burkea africana	6.68	105	*Psydrax livida*	0.44	596
	Dialium engleranum	5.61	105	*Bauhinia petersiana*	0.43	66
	Guibourtia coleosperma	2.97	6	*Burkea africana*	0.39	229
	Pterocarpus angolensis	2.09	36	*Ochna pulchra*	0.38	612
Kanovlei	*Pterocarpus angolensis*	7.27	28	*Terminalia sericea*	1.60	478
	Burkea africana	4.97	104	*Baphia massaiensis*	1.34	307
	Combretum collinum	1.13	31	*Bauhinia petersiana*	0.65	142
	Combretum psidioides	0.84	24	*Burkea africana*	0.46	232
	Commiphora angolensis	0.45	7	*Ochna pulchra*	0.35	269
Zambezi	*Baikiaea plurijuga*	16.07	51	*Combretum elaeagnoides*	1.82	600
	Combretum collinum	16.07	214	*Combretum engleri*	1.10	120
	Terminalia sericea	9.14	137	*Bauhinia petersiana*	0.69	376
	Dichrostachys cinerea	5.65	121	*Baphia massaiensis*	0.67	1164
	Combretum psidioides	2.23	72	*Grewia retinervis*	0.59	300
Kibundu	*Brachystegia spiciformis*	13.7	24	*Julbernardia paniculata*	0.28	171
	Julbernardia paniculata	7.53	27	*Pterocarpus angolensis*	0.28	153
	Isoberlinia angolensis	5.71	18	*Terminalia brachystemma*	0.11	183
	Brachystegia boehmii	3.94	12	*Albizia antunesiana*	0.09	24
	Parinari curatellifolia	1.85	5	*Diplorhynchus condylocarpon*	0.09	61
Mikembo	*Julbernardia paniculata*	22.77	165	*Julbernardia globiflora*	0.29	240
	Brachystegia boehmii	18.9	186	*Triumfetta dekindtiana*	0.25	702
	Marquesia macroura	18.11	14	*Dalbergia boehmii*	0.23	192
	Pterocarpus tinctorius	9.77	52	*Diplorhynchus condylocarpon*	0.19	133
	Diplorhynchus condylocarpon	8.35	91	*Julbernardia paniculata*	0.12	106

layer contributes to stand-level AGB by an average of 19% and 27% respectively in the woodlands and savannas of Namibia. Our results highlight the substantial increase in total AGB when including trees and shrubs with a DBH <5 cm or <10 cm, especially in dry woodlands.

4.1.1. Variation in AGB across rainfall gradient

Our results show that overall AGB increases with MAP. Previous studies have shown the positive effect of rainfall on AGB in Miombo woodlands (Godlee et al., 2021; Ngoma et al., 2018; Shackleton and Scholes, 2011). The AGB values reported in this study were generally within the range reported by other studies in the Miombo ecoregion. For instance, AGB in Tanzania ranged from 29.3 ± 6.5 Mg·ha^{-1} to 43.5 ± 7.0 Mg·ha^{-1} (Chamshama et al., 2004). The AGB in the Copperbelt region of Zambia was reported as 79.2 Mg·ha^{-1} by Kalaba et al. (2013). Ngoma et al. (2018) estimated 56 Mg·ha^{-1} in Kabompo, 39 Mg·ha^{-1} in Namwala, and 25 Mg·ha^{-1} in Sesheke in Zambia. The AGB value in Mikembo was notably higher compared to other values reported in wet woodlands probably because the Mikembo reserve has been protected from fire since 2003.

Fire suppression and protection from harvesting at Mikembo have likely facilitated the accumulation of overstorey biomass. However, the long-term exclusion of fire has indirectly reduced understorey biomass by promoting a dense overstorey canopy, which limits light availability to the understorey. This demonstrates that fire management not only influences total above-ground biomass but also alters the balance of biomass between overstorey and understorey layers. These findings underscore the complex interactions between fire regimes, light availability, water availability and vegetation structure in shaping Miombo woodland dynamics.

4.1.2. Contribution of each layer to the total AGB

The contribution of the understorey to total AGB was higher in Namibia than in DRC and decreased with MAP. The understorey AGB (<5 cm DBH) measured in this study ranged from 1.3 Mg·ha^{-1} in Kibundu to 8.7 Mg·ha^{-1} in Zambezi (Table 1). The percentage of AGB stored by the understorey layer ranged from 1.5% in Mikembo to 28.2% in Kanovlei (Fig. 7). Kanovlei, the most arid site, receives MAP of ~550 mm and is prone to fire disturbance, which promotes a sparse, open canopy. Mayr et al. (2018) found that fire disturbance in this region affected vegetation structural parameters such as the height of woody species. In addition, fire also reduces the canopy tree density allowing more light to reach the soil and favouring the growth of the understorey layer. As indicated by Kindermann et al. (2022), the fraction of AGB stored by the small-size classes increases in more open and disturbed vegetation. Our LME results support this, showing a negative influence of the overstorey basal area on the percentage of AGB stored by the understorey layer (Fig. 9). This aligns with previous studies suggesting that understorey AGB might not be responsive to stand age *per se*, but rather depends on overstorey biomass, overstorey basal area, forest management, anthropogenic disturbance, altitude, and soil conditions (Ahmad et al., 2019; Dar and Sundarapandian, 2015; Zhang et al., 2017). The accumulation of AGB in the overstorey layer indicates a concentration of resources and energy within the larger individuals. Notably, the number of shrubs and small trees does not decline with increasing rainfall, but the large trees get larger, increasing the overall AGB contribution of large trees.

4.2. Floristic composition, species diversity and woody density across forest layers and sites

To our knowledge, this is the first study addressing the co-variation of understorey and overstorey diversity, as well as the variation in the abundance and diversity of plant growth forms (shrubs and trees) across rainfall gradients in Miombo ecoregion.

The small size classes contain the most woody plant diversity, suggesting that the lower-height strata are crucial habitats for a diverse array of plant species and serve as a reservoir of plant diversity. Moreover, they indicate dynamic processes within the ecosystem, reflecting ongoing growth and regeneration. However, repeated harvesting may drastically reduce the population of large trees and favour the growth of small trees and shrubs (Muvengwi et al., 2020), as observed in Kibundu village in DRC.

4.2.1. *Total species richness*

The total species richness in this study ranged from 18 to 53 species within each plot. The species composition observed in this study matches previous findings in Miombo woodlands (Gonçalves et al., 2017; Muvengwi et al., 2020). The prevalence of Fabaceae species observed across Namibia and DRC woodlands aligns with earlier studies conducted in Zambezian woodlands and in Namibia (Frost, 1996; Godlee et al., 2020; Kazaba et al., 2020; Muledi et al., 2016).

4.2.2. *Overstorey and understorey species diversity*

Our study reveals that woody plant diversity in dry woodlands can be significantly underestimated when the understorey is not included. Despite the larger plot size used for overstorey assessments, we found that the understorey species richness in dry woodlands was equal to or higher than that in the overstorey. This contrasts with the wet Miombo, where overstorey species richness was higher.

Understorey Shannon-Wiener index (H') results for all sites were 2.0 or higher, indicating that the sites have medium to high diversity (Kalaba et al., 2013). However, no significant differences in H' and J were detected for the understorey layer across the sites. This lack of variation among sites suggests that understorey diversity remains relatively stable across environmental gradients. This stability underscores the importance of understorey vegetation as a key indicator of biodiversity and ecological resilience, regardless of site-specific conditions.

Overstorey tree species richness and overstorey Shannon-Wiener index results increased with rainfall. This result aligns well with the findings by Godlee et al. (2021) and Davies et al. (2023) across southern African savannas and woodlands, who observed that areas with greater rainfall contained more tree species. The energy-richness hypothesis (Currie et al., 2004) can be proposed to explain the positive relationships between rainfall and species richness in Miombo woodlands. Indeed, increased water availability enhances the resources and energy available to plants, leading to an increase in both the number of individuals and species. This is supported by our findings, where the overstorey woody plant density and species richness increased with rainfall. There may also be historical factors at play, with the ancestral angiosperm niche being located in wet tropical areas, accompanied by phylogenetic niche conservatism for these ancestral habitats (Augusto et al., 2014; Keil and Chase, 2019; Neves et al., 2020).

A significant difference in overstorey evenness was detected only between Kibundu (0.8) and Mikembo (0.6), despite both areas having the same range of MAP. The canopy in Kibundu is more open than in Mikembo because of historical disturbances (fire and wood harvesting). Many of the species present in the intermediate height classes and in the understorey layer in the Mikembo site may be shade tolerant. The more open canopy in Kibundu may favour the presence of various types of plants (shade-tolerant and shade-intolerant). This variety of species with different light and resource requirements can contribute to higher evenness in Kibundu, as no single species outcompete the others. In Mikembo, the competitive environment favours certain dominant species, reducing overall evenness. Additionally, the low number of trees in the intermediate height classes in Mikembo illustrates strong competition, causing trees to invest more in height growth to reach the canopy for better light capture, which is crucial for their survival and maintenance in the ecosystem.

4.2.3. *Variation in shrub and small tree species diversity across rainfall gradient*

The species diversity of small trees increases with MAP, while shrub species diversity decreases. Notably, except for the Zambezi site, shrubs had the lowest Shannon-Wiener index and species richness, with values decreasing as MAP increased. The unusually high shrub densities and species richness observed at the Zambezi site require further investigation, possibly linked to the dominance of *Combretum* and *Baphia* species, the exclusion of fire or high cattle abundance.

The decline in shrub diversity with increasing MAP aligns with findings from other continents, where high precipitation levels have been associated with a decline in shrub species richness (Martín-Queller et al., 2011). Although shrub richness is often negatively correlated with tree cover, as shrubs struggle to compete with larger trees and face limited light availability in the understorey (Moreno-Fernández et al., 2021). However, our results did not indicate a significant negative relationship between shrub species and tree cover (basal area) (Fig. 8). In dry woodlands, shrubs are more numerous, generally do not reach the overstorey and are most abundant at lower DBH classes, with their number decreasing in higher DBH classes (Moreno-Fernández et al., 2021). In contrast, wet Miombo sites in the DRC, with a higher prevalence of small trees, exhibit more species that seem to be exclusive to the overstorey. The variation in shrub and tree species proportions across the rainfall gradient may explain these patterns. Hydric stress in dry woodlands likely limits tree growth more than shrub growth, contributing to the observed distribution of species across different layers (Martín-Queller et al., 2011; Moreno-Fernández et al., 2021). However, as most research on shrub species variation has been conducted in temperate forests, further studies are needed to better understand these dynamics in the context of African woodlands.

4.3. *Future research and possible implications*

Our study was conducted at a limited number of sites within Namibia and DRC, which, while representing both extreme ends of the MAP gradient within the Miombo ecoregion, do not fully capture environmental variability across the whole ecoregion. Despite this, these sites provide valuable insights into what may prove to be general patterns and trends in biomass and species distribution. Future research should include sites with intermediate MAP values (between 700 and 1,200 mm) to offer a more comprehensive understanding of biomass distribution across forest layers and lifeforms along the rainfall gradient. Additionally, there are multiple facets to rainfall patterns, such as rainfall intensity and seasonal distribution, which may also affect biomass and species diversity. Future studies could also consider the role of socio-economic factors, fuelwood harvesting, and wildfire management in shaping vegetation structure. While the study did not explore soil fertility and microclimatic conditions, the results align with existing literature on the impact of rainfall and tree cover on biomass and diversity, reinforcing the validity of the findings.

5. Conclusion

This study aimed to describe the diversity and biomass distribution across the vertical structure of the Miombo ecoregion, including small trees and shrubs. A key contribution of this study is demonstrating that many biomass studies in African woodlands may underestimate total biomass by an average of 18.3% when trees and shrubs with a DBH <5 cm are excluded, particularly in dry woodlands. The research highlights the importance of including different lifeforms to get more accurate biomass estimates. Furthermore, the study demonstrates how rainfall gradients impact species richness and biomass distribution, with significant implications for forest management and conservation strategies.

The findings from this study have several important applications and implications for forest management and conservation in Miombo ecoregion. By highlighting the significant contribution of the understorey to total AGB, particularly in dry woodlands, this research underscores the necessity of including smaller trees and shrubs in biomass assessments for more accurate biomass stock estimates. Additionally, it highlights the importance of understorey species in biodiversity assessments, particularly in dry woodlands where understorey species richness was equal to or greater than that of the overstorey.

CRediT authorship contribution statement

Hermane Diesse: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **John L. Godlee:** Writing – review & editing, Supervision, Investigation, Conceptualization. **Nichola Knox:** Writing – review & editing, Conceptualization. **Jonathan Muledi:** Writing – review & editing, Investigation. **Leena Naftal:** Writing – review & editing, Investigation. **David Nkulu:** Writing – review & editing, Investigation. **Ben Nkomba:** Writing – review & editing, Investigation. **Gabriel Uusiku:** Writing – review & editing, Investigation. **Kyle Dexter:** Writing – review & editing, Investigation. **Vera De Cauwer:** Writing – review & editing, Investigation, Conceptualization.

Availability of data and materials

The datasets used and/or analysed during the current study are available from the corresponding author upon reasonable request.

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.fecs.2025.100302.

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