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Leaf habit, maximum height, and wood density of tropical woody flora in Africa: phylogenetic constraints, covariation, and responses to seasonal drought

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Author Contributions

A.-P. Gorel designed the study and conducted the research. A.-P. Gorel and A. Fayolle compiled data on species traits and A. Fayolle provided expertise on functional ecology. A.-P. Gorel, G. Ligot, V. Rossi, and O.J. Hardy performed the phylogenetic analyses. H. Beeckman provided the data for wood density and expertise on wood traits, K. Steppe provided expertise on hydraulic strategies. All authors participated in the interpretation of the results. A.-P. Gorel wrote the manuscript, and all authors made significant contributions to the revisions.

Data availability statement

The trait database (including leaf habit and maximum height) is available online in Dryad https://doi.org/10.5061/dryad.q573n5ttn

Conflict of interest statement

The authors declare no conflict of interest.

Summary

1. How woody floras have evolved to cope with seasonal drought is still poorly known, especially in tropical Africa, which experiences a drier and more seasonal climate compared to other tropical regions.

2. Here, we characterized the phylogenetic and climatic distribution of three key traits associated with desiccation avoidance or tolerance, focusing on self-supporting woody species of tropical African forests and savannas. We assembled a large database with newly compiled data on species leaf habit (evergreen *vs* deciduous, 1,255 species) and maximum height (1,281 species), along with new data on oven-dry wood density (1,363 species), climatic niche, and phylogenetic relatedness. Bayesian phylogenetic mixed models were used to assess the phylogenetic signal in niches and trait attributes, to explore individual trait responses to climate and to investigate trait covariations, both in general and for each characterisation of the climatic niche. To date, this study represents the first quantitative assessment of the phylogenetic signal in the species leaf habit for the woody flora of tropical Africa, though drought deciduousness is widespread in seasonal forests and savannas.

3. We identified a strong phylogenetic signal, notably for species biome affinity and leaf habit, but also major evolutionary changes. Relying solely on climate was found to be ineffective for predicting species wood density and insufficient for accurately predicting species leaf habit or maximum height. Among forests, the effect of climate on leaf habit became evident when considering covariations with maximum height or wood density. Small understory species are more likely to be evergreen with dense wood, while canopy species are more likely to be deciduous with light wood. This general pattern varies with climate as both evergreen and deciduous species coexist in the canopy of the wettest sites.

4. Synthesis. This study provides first insights into how phylogenetic constraints and climate have shaped species traits related to drought strategies for the woody flora of tropical Africa. It pioneers the modelling of leaf habit in relation to maximum tree height and wood density, considering numerous species and their phylogenetic relationships.

Keywords

Adaptation, Africa, Climatic niche, Deciduous, Evergreen, Phylogenetic signal, Traits, Tropical biomes.

Introduction

The increase in extreme climatic events, such as droughts and heat waves, induces serious tree mortality around the world (Hartmann et al., 2022) and is expected to worsen dramatically in the coming decades (Thiery et al., 2021). Predicting how trees will respond to these changes is crucial and requires an understanding of the functional processes governing species drought vulnerability (Brodribb et al., 2020). In recent decades, efforts have been made to improve our knowledge of the drought-related strategies for tropical trees, but the lack of data in Africa is alarming (Oliveira et al., 2019). There is an urgent need to focus on African forests and savannas, which together cover around 10% of the world's land area and are characterized by drier and more seasonal climates than other tropical regions (Silva de Miranda et al., 2022).

Deciduousness provides a clear advantage in seasonally dry environments. It halts transpiration and prevents xylem embolism, reducing the risk of hydraulic failure (McDowell et al., 2008)—a major cause of tropical tree mortality (Rowland et al., 2015). Deciduousness is likely a crucial desiccation avoidance strategy for many tropical tree species (Oliveira et al., 2021). In central Africa, the percentage of deciduous trees in forest plots has been shown to increase with the severity of the dry season (Ouédraogo et al., 2016). A marked gradient in deciduousness has long been recognized between wet evergreen forests in Gabon and the vast area covered by semi-deciduous forests further inland (Aubréville, 1968; White, 1979). A recent analysis of commercial forest inventories across the region confirmed this spatial pattern and estimated the percentage of deciduous trees to vary between 10% in wet evergreen forests to approximately 60% in the drier and more seasonal forests (Réjou-Méchain et al., 2021). The relationship between forest deciduousness and climate can however be altered by soil fertility (Oliveira et al., 2021; Ouédraogo et al., 2016), as nutrient-poor soils favour species with long-lived leaves, minimizing nutrient costs and outcompeting deciduous species in short growing periods (Aerts, 1995). In African savannas, which are found under drier and more seasonal climates than forests (Aleman et al., 2020), the deciduous leaf habit dominates, as separately reported for the Sudanian (de Bie et al., 1998; Seghieri et al., 2012) and the Zambezian (Chidumayo & Gumbo, 2010) regions.

Under similar climatic and soil conditions, deciduous species are likely to adopt a more acquisitive strategy than evergreen species (Markesteijn & Poorter, 2009; Oliveira et al., 2021 and references therein). The loss of leaves indeed results in a loss of energy, as photosynthesis is interrupted, and to compensate, deciduous species must exhibit hydraulic and photosynthetic efficiency during a shorter growing season. Acquisitive strategy has been related to lower wood density (Reich, 2014; Wright et al., 2010) and increased xylem susceptibility to embolism (Oliveira et al., 2021). However, the impact of increased embolism sensitivity on the fitness of deciduous species could be minimal, given their ability to avoid critical drops in water potential by shedding their leaves during the dry season. In contrast, to tolerate seasonal drought, evergreen species should adopt a more conservative strategy, allocating their resources to denser, more embolism-resistant sapwood tissues (Choat et al., 2005; Hacke et al., 2001; Oliveira et al., 2021). Wood density can therefore be considered as important trait in tree drought research, and is studied globally (Chave et al. 2009), including in Africa (Maniatis et al., 2011). Yet conflicting evidence for tropical trees exists regarding its relationship with climate. Some studies report an increase in wood density with decreasing rainfall (e.g. Fayolle et al., 2016; Ibanez et al., 2017), while the opposite (e.g. Barbosa & Fearnside, 2004; Maharjan et al., 2011) and no trend have also been reported, the latter referring to other determinants of wood density such as soils (Gourlet-Fleury et al., 2011) and disturbance (Réjou-Méchain et al., 2021).

The investment by deciduous species in lighter wood with potentially wider vessels may enable them to attain greater heights (Fajardo, 2022, 2022; Liu et al., 2015; Olson et al., 2018) compared to evergreen species, which should prioritize denser tissues resulting in an increase in hydraulic resistance that may physically limit height (Koch et al., 2004). This contrast between tall deciduous and small evergreen species has already been reported in moist forests of central Africa where tall canopy species are typically deciduous and coexist with small evergreen understory species (Loubota Panzou et al., 2018). The advantage of a taller stature is evident in forest environments where individuals compete for light (Kitajima & Poorter, 2010) and in savannas where height growth allows for escaping crown damage resulting from browsing and low-intensity fires (i.e. the escape height, Dantas & Pausas, 2013). Concerning small species, they evolved toward other traits in forests, such as producing tough, well-protected leaves, increasing lifetime carbon gain while limiting self-shading to tolerate shade in understory (Kitajima & Poorter, 2010; Sterck et al., 2006); and in savannas, they developed thorns or shrubby forms to prevent browsing or have invested in thick bark to survive fires (Charles-Dominique et al., 2016).

In addition to varying with environmental conditions, traits often display a high phylogenetic signal, indicating that phylogenetically related species tend to share similar attributes and occupy similar environments (Blomberg & Garland, 2002). This signal emerges when traits have evolved only gradually through small changes driven by genetic drift and fluctuating directional selection, or in response to weak selective pressure (Losos, 2008). In contrast, a weak phylogenetic signal is expected in traits that have undergone rapid evolutionary changes in response to environmental pressures or other forms of selection, or in traits prone to high phenotypic plasticity or measurement errors (Housworth et al., 2004). Certain traits, like phenology, show a high phylogenetic signal, as observed for flowering in the northern hemisphere (Davies et al., 2013) and in Panama (Wright & Calderon, 1995) but this pattern remains untested for the African flora. In any case, accounting for phylogeny is crucial when modelling the environmental response of species traits and strategies, as it addresses the statistical dependence among species resulting from their shared evolutionary history (Davies et al., 2013).

In this study, we aimed to characterize the phylogenetic and climatic distribution of three key traits associated with two dominant ecological strategies to cope with drought: desiccation avoidance and tolerance. Traits include leaf habit (deciduous vs. evergreen), maximum height, and wood density. Based on existing information on species climatic niche (defined here as the *potential niche* according to Guisan et al. (2014)) and biome affinity (Gorel et al., 2022), on phylogenetic relatedness (Janssens et al., 2020), and on an extensive compilation of traits, we specifically addressed the following research questions. (1) What is the strength of the phylogenetic signal in climatic niches and traits? (2) How do traits vary across climates? (3) To what extent is the response of leaf habit to dry and seasonal climatic conditions influenced by species stature and wood density? We hypothesised that the probability of a species being deciduous increases with climatic water deficit (*i.e.* the water lost by the environment during dry months), given the significant advantages of this strategy in drier environments to avoid run-away xylem embolism. Furthermore, within the same climate, we hypothesise that species probability to be deciduous increases with maximum tree height and inversely with wood density. Deciduous species, which avoid drought, are expected to invest in lighter wood and to reach greater heights (Fajardo, 2022). In contrast, evergreen species invest in denser wood with expected higher tolerance to embolism formation, increased hydraulic resistance and maximum height limitation.

Materials and methods

Climatic niche

In a previous study, 3,136 self-supporting (*i.e.* excluding climbers) woody species from tropical Africa were previously assigned to two broad groups corresponding to the forest and the savanna biomes and six phytoclimatic groups when describing their climatic niches at a finer resolution (Gorel et al., 2022). These groups were delineated based on species niche similarity. The niches were modelled using the methods described in Broennimann et al. (2012), using published occurrence data from the RAINBIO database (Dauby et al., 2016), complemented with tree species lists in forest (Fayolle et al., 2014) and savanna (Fayolle et al., 2019) sites, along with climatic spatial data (CMCC-BioClimInd data set, Noce et al., 2020). Species were then grouped according to their niche similarity using a hierarchical clustering approach with Ward's algorithm. We re-analysed this dataset to distinguish, in addition to species characteristic of a given biome or phytoclimatic group, generalist species whose distribution covers both biomes (Aleman et al., 2020) and forest generalist or savanna generalist species whose distribution covers all forest or savanna phytoclimatic groups. This led us to recognize three species groups according to the biome affinity and eight phytoclimatic groups These groups are differentially exposed to dry and seasonal climatic conditions according to the Climatic Water Deficit index (CWD, Fig. 1), which quantifies the environmental water loss during dry months (defined as months where evapotranspiration exceeds rainfall) by summing the positive differences between monthly potential evapotranspiration and precipitation over one year. Potential evapotranspiration was derived from monthly minimum and maximum temperatures (Droogers & Allen, 2002). Temperature data were from WorldClim (Hijmans et al., 2005), and precipitation from CHIRPS, which is calibrated with ground station data and offers higher precision (Deblauwe et al., 2016). Of the initial phytoclimatic groups assigned by Gorel et al. (2022), we removed species assigned to the coastal group. The vegetation of this coastal group forms a forest-savanna mosaic driven by complex topography. In the absence of clear hypotheses on climatic adaptation for this group, we have excluded it from our study, and, hence, considered 2,839 species assigned to biomes, phytoclimatic groups, and generalist categories.

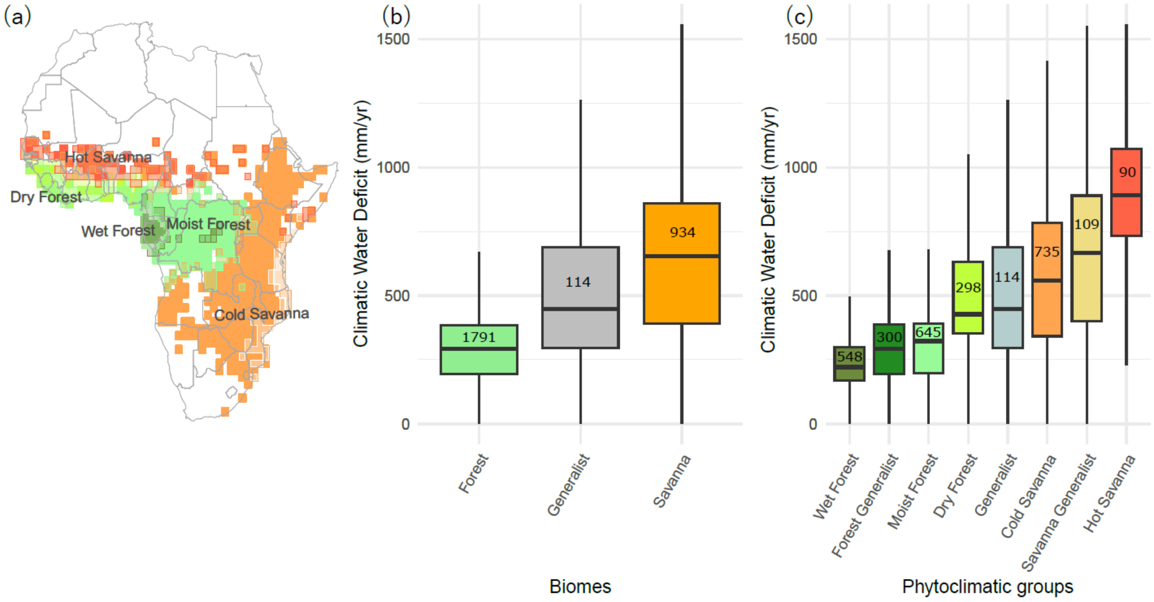

Figure 1 (a) Dominance across tropical Africa of biomes and phytoclimatic groups delineated in Gorel *et al.* (2022). Based on the pairwise niche similarity, the woody species (including trees and shrubs) were categorized into two broad groups, which represent the species biome affinity, with the forest-associated species (green colours) and the savanna-associated species (orange and red colours), as well as a generalist group corresponding to species covering both biomes (the generalist group is not represented in the map). The biomes were further divided into phytoclimatic groups: four forest groups ("wet forest" in dark green, "moist forest" in pale green, "dry forest" in yellow green and a forest generalist group), and three savanna subgroups ("cold savanna" in orange, "hot savanna" in red and a savanna generalist group). Solid colours represent areas where more than 50% of the species present in the pixel are assigned to the corresponding group. Pixels with partial transparency represent areas where more than 25%, but less than 50%, of the species present in the pixel are assigned to the phytoclimatic group. The generalist group at biome level was also included in the phytoclimatic groups. Climatic Water Deficit experienced by the woody species assigned to (b) biomes and to (c) phytoclimatic groups. Boxes denote median values and the 25th to 75th percentiles; vertical lines outside of boxes represent the 10th and 90th percentiles. The number of species assigned to each biome, phytoclimatic group and generalist category is indicated within the boxplots. Note that some zero values in Climatic Water Deficit for savanna occurrences may result from mispositioned data due to coarse resolution.

Traits

For the tropical woody flora of Africa, we compiled trait attributes at the species level for leaf habit (n=1,255 species), and maximum height (n=1,281 species) using previously published database, original studies, and flora (the list of data sources is provided in the Data sources section). For species both defined as evergreen and deciduous, the deciduous leaf habit was systematically retained as it expresses the ability of the species for leaf shedding, even barely. When multiple measures for maximum height and wood density were available, mean values were computed. Oven-dry wood density values (*i.e.*, oven-dry mass over oven-dry volume) from xylarium samples were provided by the Service of Wood Biology of the AfricaMuseum in Tervuren, Belgium (n=1,363 species). The global wood density database compiling basic density values (Zanne et al. 2009) was not retained here because it contained less information for tropical Africa. The two databases were not merged due to differences in values between the basic wood density, measured as oven dry mass to green volume, and the oven-dry wood density (Vieilledent et al., 2018), despite their expected similar response to environment. The taxonomic names follow the standards of the Tropicos database, created by the Missouri Botanical Garden. The R package TNRS was used to resolve plant taxonomic names. In all datasets, we exclusively included self-supporting species, such as trees and shrubs, while excluding climbers. As a result, the trait dataset consisted of 1,252 species for leaf habit, 1,275 species for maximum height, and 1,253 species for wood density.

Phylogeny

We used a genus-level dated Angiosperm phylogeny (8,394 genera) developed from the species-level phylogeny (36,106 species) of Janssens *et al.* (2020). We did not consider the intra-genus level because the original phylogeny is based on plastid markers which can induce false topologies within many genera due to chloroplast captures (e.g. Boom et al., 2021 for *Brachystegia* and references therein). The phylogeny recognizes some *Vachellia* and *Senegalia* species but has not revised the taxonomy for all the African species previously named *Acacia*, especially those we studied. Therefore, we have updated the phylogeny to reflect the reclassification into *Vachellia* or *Senegalia*, as proposed by Kyalangalilwa et al. (2013).

The distribution of biomes and trait attributes across the phylogeny was investigated. The number of species and genera examined varied based on the alignment of traits, biomes, and phylogeny (Table 1). For example, out of the initial dataset of 2,839 species assigned to biomes or phytoclimatic groups, 2,630 species were represented by genera included in the phylogeny. The 499 species included in the phylogeny, with information on biomes (or phytoclimatic groups) and for the three traits, are presented in Fig. 2. For each trait, the values for all species with data are presented alongside the phylogeny in Appendix 1 in SI. An overview figure showing how the whole data are distributed across the phylogeny is also included in Appendix 1. The number of species considered for each trait in each biome or phytoclimatic group is provided in Fig. 3, along with the data distribution. This includes the proportion of deciduous *vs.* evergreen species, as well as the distribution of wood density and maximum height attributes.

Statistical analysis

We constructed three sets of Bayesian phylogenetic mixed models (“MCMCglmm” R package, version 2.34, Hadfield, 2010), each set addressing one of our research questions. In the first set (Table 1, M1 to M5), we structured the models to evaluate the phylogenetic and non-phylogenetic variances in the species climatic niche and trait, individually. The second set (M6 to M11) aimed to assess the relationships between the species traits and the climatic niche (*i.e.*, the trait response to climate). In the third set (M12 to M20), we explored the overall trait covariations, and the trait covariations within climatic niches.

In the first model set (M1 to M5), the species climatic niches (biomes or phytoclimatic groups) and the traits (leaf habit, maximum height, and wood density) were individually modelled including only random effects, *i.e.*, the genus-level phylogeny and the genus identity. Following the method outlined in Sanchez-Martinez *et al.* (2020), these models allowed the variance to be partitioned into three components: (1) the phylogenetic variance, quantifying the proportion of variance in the niche/trait attributes explained by phylogenetic relationships among genera; (2) the non-phylogenetic intergeneric variance, quantifying the proportion of variance not explained by the phylogenetic relationships between genera; (3) the intrageneric variance which corresponds to the residual variance of the models, quantifying the proportion of variance caused by intra-genus variability in trait. The phylogenetic variance gives a measure of the phylogenetic signal, also called the “*phylogenetic heritability*” following Housworth *et al.* (2004). The non-phylogenetic and intrageneric variances could result from rapid evolutionary changes in response to the environment or other forms of selection, “*the nonheritable component*” of Housworth *et al.* (2004). Preliminary analyses, including simulations of Brownian evolution and randomization of trait attributes (Appendix 2 in SI), as well as classical assessments of phylogenetic signal using phylogenetic distograms (Hardy & Pavoine, 2012) and phylogenetic signal statistics (Münkemüller et al., 2012; results not shown), were conducted to validate the consistency of variance partitioning and our interpretation of the results.

In the second model set (M6 to M11), each trait (leaf habit, maximum height, and wood density) was individually modelled in response to biome (or phytoclimatic group) as fixed effect. The genus-level phylogeny and genus identity were included as random effects. We analysed model coefficients and performed pairwise tests of factor contrasts using the "emmeans" R package (Lenth et al., 2021). We quantified the marginal variance (R^2m), representing the part of variance explained by fixed effects (Nakagawa & Schielzeth, 2013), as well as the remaining proportion of phylogenetic, non-phylogenetic and intergeneric variances.

In the last model set (M12 to M20), we explored the pairwise covariations between traits. Specifically, leaf habit was modelled in response to maximum height (M12) or oven-dry wood density (M15). Then, we expanded these models by introducing the climatic niches (biomes or phytoclimatic groups) and its interaction with maximum height (M13 and M14) or wood density (M16 and M17) as fixed effects. We also examined how maximum height was related to oven-dry wood density (M18 to M20). All these models had the same random structure as the previous models, including two random effects: phylogeny at the genus level and genus identity. The marginal, phylogenetic, non-phylogenetic and intergeneric variance were also quantified.

Biomes and phytoclimatic groups were modelled as ordinal variables, ordered by increasing Climatic Water Deficit (using the median; Fig. 1). Leaf habit was modelled as a categorical variable. Log-transformed maximum height and wood density were modelled as continuous variables with a Gaussian distribution. We ran the MCMC algorithm for 400,000 iterations with a burn-in of 200,000 and collected every 200 sample to thin the chain. In addition, to ensure that we used a sufficient number of iterations, we calibrated a complex model (M14) with 6 million iterations (burn-in = 2 million, thin = 4,000). We found virtually no difference in the results and the variance partition compared with the model calibrated with 400,000 iterations. For each model, the number of species (and corresponding genera) used for calibration is presented (Table 1) and corresponds to those species that have values for the climatic niche and/or trait considered and whose genus is included in the phylogeny.

Results

Table 1. Variance partitioning for the models tested. All models consider phylogeny at the genus level and genus identity as random effects. The percentages of mean variance, and the lower and upper 95% confidence intervals (in square brackets) are shown, as well as the number of species and genera used to calibrate the models. The number of species and genera examined varied depending on the alignment of climatic niches, traits and phylogeny. The marginal variance is the variance explained by fixed effects. Abbreviations corresponds to phytoclim: phytoclimatic groups, WD: oven-dry wood density, and hmax: maximum height.

Model set	*Model*	*Variable to explain and fixed effects*	*Species (n)*	*Genus (n)*	*Phylogenetic variance (%)*	*Non-phylo. intergeneric variance (%)*	*Intrageneric variance (%)*	*Marginal variance (%)*
1. Phylo. and non-phylogenetic components	M1	*biomes ~ 1*	2630	627	67.51 [48.73 : 84.58]	17.91 [1.81 : 32.33]	14.57 [10.15 : 19.17]	-
	M2	*phytoclim ~ 1*	2630	627	50.75 [34.57 : 65.82]	17.5 [4.84 : 29.03]	31.75 [26.19 : 37.8]	-
	M3	*leaf_habit ~ 1*	1159	478	70.66 [43.53 : 93.04]	19.82 [0.03 : 44.64]	9.52 [5.47 : 14.01]	-
	M4	*Log(hmax) ~ 1*	1195	469	56.15 [43.32 : 68.03]	6.43 [0.43 : 14.77]	37.42 [30.52 : 43.9]	-
	M5	*WD ~ 1*	1160	462	50.96 [38.36 : 63.95]	17.23 [8.98 : 27.72]	31.81 [26.6 : 37.75]	-
2. Traits response to climate	M6	*leaf_habit ~ biomes*	870	375	73.77 [49.37 : 90.06]	8.08 [0.02 : 28.82]	9.75 [5.3 : 14.27]	8.4 [3.23 : 13.97]
	M7	*leaf_habit ~ phytoclim*	870	375	66.08 [43.03 : 85.85]	10.13 [0.02 : 30.52]	8.33 [4.84 : 12.52]	15.46 [8.41 : 23.16]
	M8	*Log(hmax) ~ biomes*	947	385	46.02 [32.54 : 56.49]	4.39 [0.31 : 11.15]	39.37 [32.38 : 46.72]	10.22 [6.95 : 13.93]
	M9	*Log(hmax) ~ phytoclim*	947	385	46.28 [33.59 : 57.94]	4.09 [0.38 : 10.52]	38.58 [31.49 : 45.87]	11.05 [7.75 : 14.71]
	M10	*WD ~ biomes*	872	370	46 [32.26 : 62.36]	21.77 [9.86 : 32.98]	32.04 [26.24 : 38.15]	0.2 [0 : 0.6]
	M11	*WD ~ phytoclim*	872	370	45.75 [31.53 : 61.51]	21.15 [9.54 : 32.33]	32.32 [25.77 : 38.66]	0.78 [0.13 : 1.49]
3. Trait covariations	M12	*leaf_habit ~ hmax*	875	389	67.96 [34.42 : 93.96]	21.23 [0.02 : 51.17]	9.63 [5.49 : 15.01]	1.18 [0 : 3.17]
	M13	*leaf_habit ~ biomes + biomes:hmax*	715	334	52.22 [22.34 : 74.79]	11.04 [0.02 : 34.13]	12.88 [7.18 : 18.62]	23.86 [13.19 : 35.22]
	M14	*leaf_habit ~ phytoclim + phytoclim:hmax*	715	334	41.46 [17.73 : 64.1]	6.88 [0.02 : 24.32]	10.55 [6.19 : 15.25]	41.11 [27.42 : 55.72]
	M15	*leaf_habit ~ WD*	646	327	69.93 [45.94 : 88.89]	7.88 [0.03 : 29.74]	16.45 [8.75 : 25.36]	5.74 [0.51 : 11.71]
	M16	*leaf_habit ~ biomes + biomes:WD*	577	295	62.88 [38.53 : 83.06]	7.1 [0.03 : 26.46]	14.97 [7.21 : 24.17]	15.05 [6.22 : 25.09]
	M17	*leaf_habit ~ phytoclim + phytoclim:WD*	577	295	53.39 [24.05 : 75.55]	10.19 [0.02 : 30.9]	9.31 [4.65 : 14.71]	27.12 [14.54 : 40.21]
	M18	*lnhmax ~ WD*	659	327	39.49 [25.3 : 54.32]	6.63 [0.39 : 16.24]	52.41 [41.64 : 63.08]	1.46 [0 : 3.27]
	M19	*log(hmax) ~ biomes + biomes:WD*	588	294	36.32 [23.1 : 48.05]	3.67 [0.26 : 9.05]	45.76 [36.13 : 56.03]	14.25 [9.65 : 19.37]
	M20	*log(hmax) ~ clim + clim:WD*	588	294	36.65 [22.96 : 47.75]	3.32 [0.35 : 8.36]	44.37 [35.47 : 54]	15.66 [10.2 : 20.32]

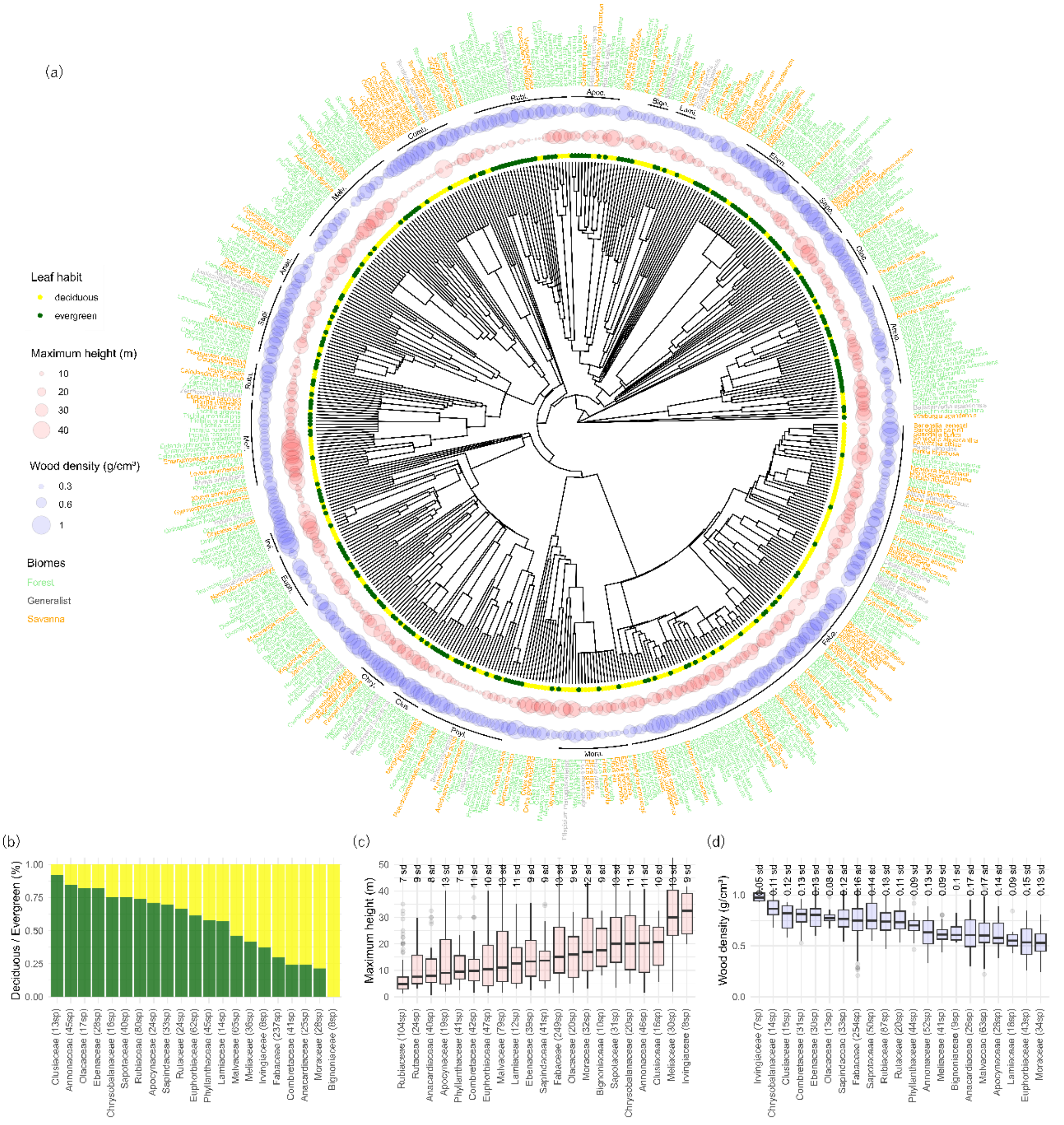

Figure 2 Phylogeny, traits, and biomes. (a) The phylogram shows associations between biomes and traits, *i.e.*, leaf habit (inner circle, yellow and dark green dots for deciduous and evergreen, respectively), maximum height (red dots whose size represents the variation), and wood density (blue dots whose size represents the variation) at species level (the species were attached to the genus-level phylogeny as polytomies for illustrative purposes). The species names are coloured according to their biomes (forest in green, savanna in orange, generalist in grey). Only species (n=499) that have information available for the biomes and the three traits are considered here and abbreviated names are shown for family with more than five species. Details on the distribution per families, for families with more than five species in the phylogram, are given for (b) leaf habit,

(c) maximum height and (d) wood density. Boxes denote median values and the 25th to 75th percentiles; horizontal lines outside of boxes represent the 10th and 90th percentiles. The number of species (sp) and the standard deviation (sd) are given.

Phylogenetic and non-phylogenetic components

When partitioning the variance between phylogenetic and non-phylogenetic components (M1 to M5, Table 1, Fig. 3a, 3d, 3g), the phylogenetic variance was found substantial (considered in this case as a measure of phylogenetic signal) for both the species climatic niches (68% of the total variance for biomes, 51% for phytoclimatic groups) and traits (71% for leaf habit and 56% and 51% for maximum height and wood density, respectively). Large parts of the phylogeny appeared dominated by a certain climatic niche or certain trait attributes (Fig. 2). For example, the evergreen leaf habit was predominantly shared among species in the Clusiaceae and the Annonaceae families, whereas the deciduous leaf habit was dominant in the Bignoniaceae and Moraceae families (Fig. 2a and b). Climatic niches, leaf habit and wood density showed similar non-phylogenetic intergeneric variance (around 17% of the total variance, Table 1). Intrageneric variances were low for leaf habit (around 9%) compared to phytoclimatic group, wood density and maximum height (around 35%, Table 1) for which rapid evolutionary changes within genera could be substantial.

Trait response to climate

Concerning the probability to be deciduous, the climatic niche explained only a small part of the variability (marginal variance of 8% for biomes and 15% for phytoclimatic groups, M6 and M7 in Table 1, Fig. 3a). The probability to be deciduous was, however, significantly lower for forest than for savanna species (0.27 *vs* 0.47, M6, Fig. 3b) and increased progressively with Climatic Water Deficit for forest phytoclimatic groups, while remaining consistently high for all savanna phytoclimatic groups (M7, Fig. 3c). It is worth noting that the phylogenetic variance was 71% in M3 and decreased to 66% in M7 (Fig. 3d, Table 1). Since M7 was built on M3 by including phytoclimatic group as fixed effect, this suggests that part of the phylogenetic signal in leaf habit is linked to lineage preference for phytoclimatic group, *i.e.*, some parts of the phylogeny consist of related species that share both the same leaf habit and the same phytoclimatic group. In contrast, the phylogenetic variance was 74% in M6 (biome as fixed effect), which is similar to that of M3 (with no significant difference according to the 95% confidence intervals). This suggests that parts of the phylogeny comprise related species that occupy the same biome (as indicated by the high phylogenetic variance in M6) but do not necessarily share the same leaf habit, or *vice versa*.

Concerning the maximum height, the climatic niche also accounted for a relatively small part of the variability (marginal variance around 10% for both biomes and phytoclimatic groups, M8 and M9 in Table 1). Maximum height was significantly higher for forest than for savanna species (16 m *vs* 9 m in average, Fig. 3e). As outlined for leaf habit, the small decrease in phylogenetic variance when including biomes or phytoclimatic groups as fixed effects (M4 vs. M8, M9) suggests that part of the phylogenetic signal in maximum height is related to lineage preferences for specific biomes or phytoclimatic groups.

Concerning wood density, including biomes or phytoclimatic groups in the models did not noticeably affect the partition of variance (with marginal variance being less than 1% in M10 and M11, Table 1, Fig. 3h, 3i). Consequently, we did not identify any significant differences in wood density among biomes or phytoclimatic groups.

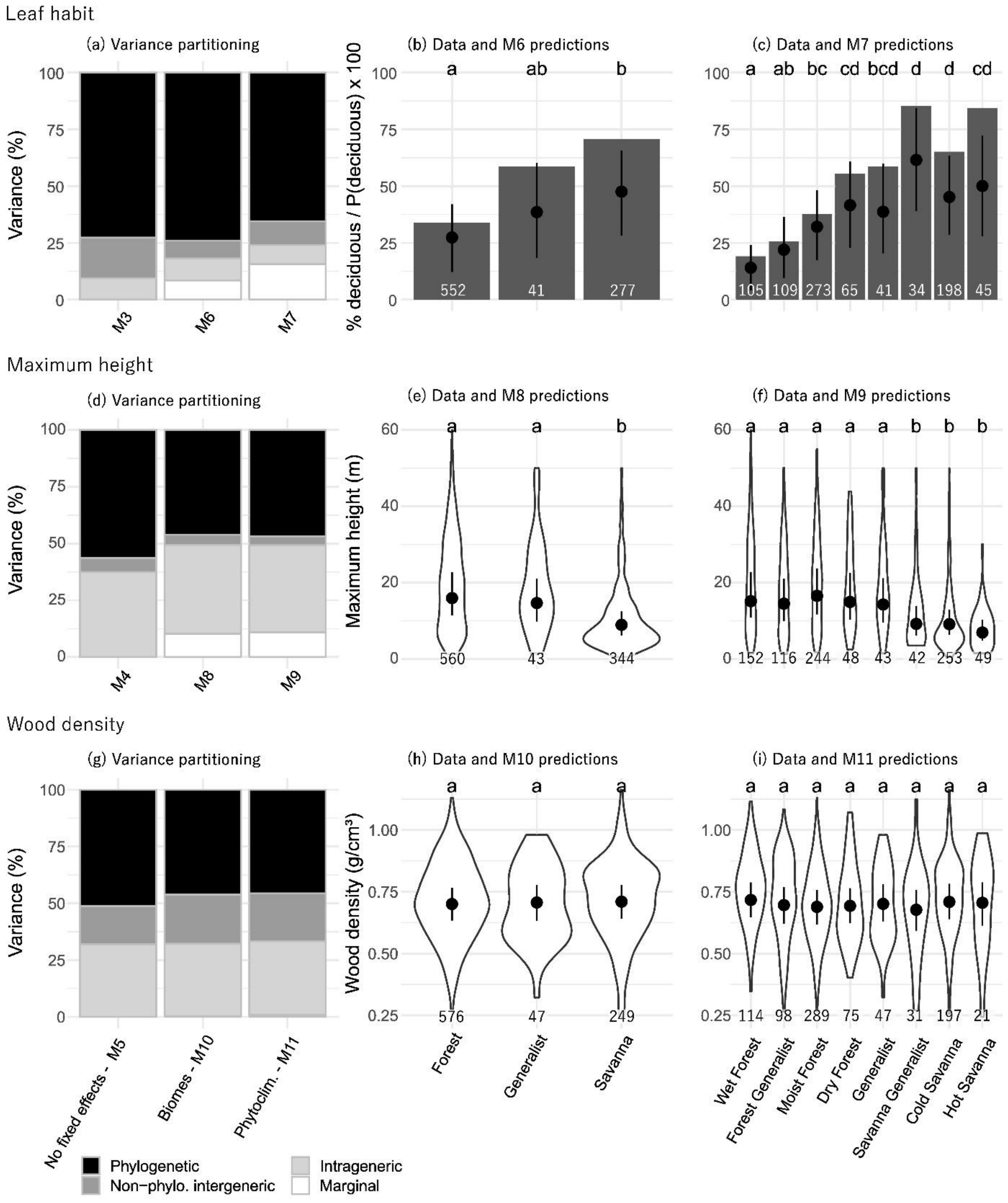

Figure 3 Variance partitioning (left panels), data distribution (bar- or violin-plots) and model predictions without random effects (points with confidence intervals) for (a, b, c) leaf habit, (d, e, f) maximum height, and (g, h, i) wood density according to biomes (b, e, h) and phytoclimatic groups (c, f, i). The letters above model predictions identify groups that are not significantly different according to pairwise comparison of contrasts. The marginal variance is the variance explained by fixed

effects. The number of species with trait values for each biome or phytoclimatic group, along with a phylogenetic match, is indicated directly below each bar or violin plot.

Trait covariations

When exploring trait covariations, we found that the biome (or phytoclimatic group) and its interaction with maximum height explained 24% (or 41%) of the variance in leaf habit (marginal variance in M13 and M14, Table 1). It should be noted that the contribution of maximum height alone, without accounting for its interaction with biome or phytoclimatic group, explained only 1% of the variability in leaf habit (M12). This emphasises that the relationship between leaf habit and maximum height becomes significant only when considered within the context of a specific biome or phytoclimatic group. In the forest biome, the probability to be deciduous increased with maximum height (Fig. 4b), from 0.15 for understory species (~ 5 m high) to more than 0.50 for emergent tree species (≥ 40 m high). This trend was shared by all forest phytoclimatic groups (Fig. 4c): the drier the group, the higher the probability to be deciduous. The wet forest species reach 40 m tall with a relatively low probability (0.25) to be deciduous, the moist or dry forest species which reach more than 40 m are most likely deciduous (0.65 and 0.80, respectively). For generalist and savanna species (Fig. 4b), as well as for cold savanna species at a finer resolution (Fig. 4c), the probability to be deciduous remained high, and there was no apparent relationship between leaf habit and maximum height. In contrast, among savanna generalists and hot savanna species, a different trend is observed: species generally exhibit a smaller stature compared to those in forests, and the probability to be deciduous decreases with increasing maximum height (Fig. 4c).

When wood density was considered instead of maximum height for predicting leaf habit, the marginal variance was lower (15% for biomes and 27% for phytoclimatic groups, Table 1) and the trends were reversed (*i.e*. the probability of being deciduous decreased as wood density increased) except for the savanna generalist and the dry forest species. For the forest biome, the probability to be deciduous was greater for light wood species (Fig. 4e and f). This result was largely explained by the inverse relationship between maximum height and oven-dry wood density observed for all species (Fig. 4g, h, i). Differences in stature were maintained between forest and savanna species, with forest species being taller than savanna species for the same wood density (Fig. 4h, i).

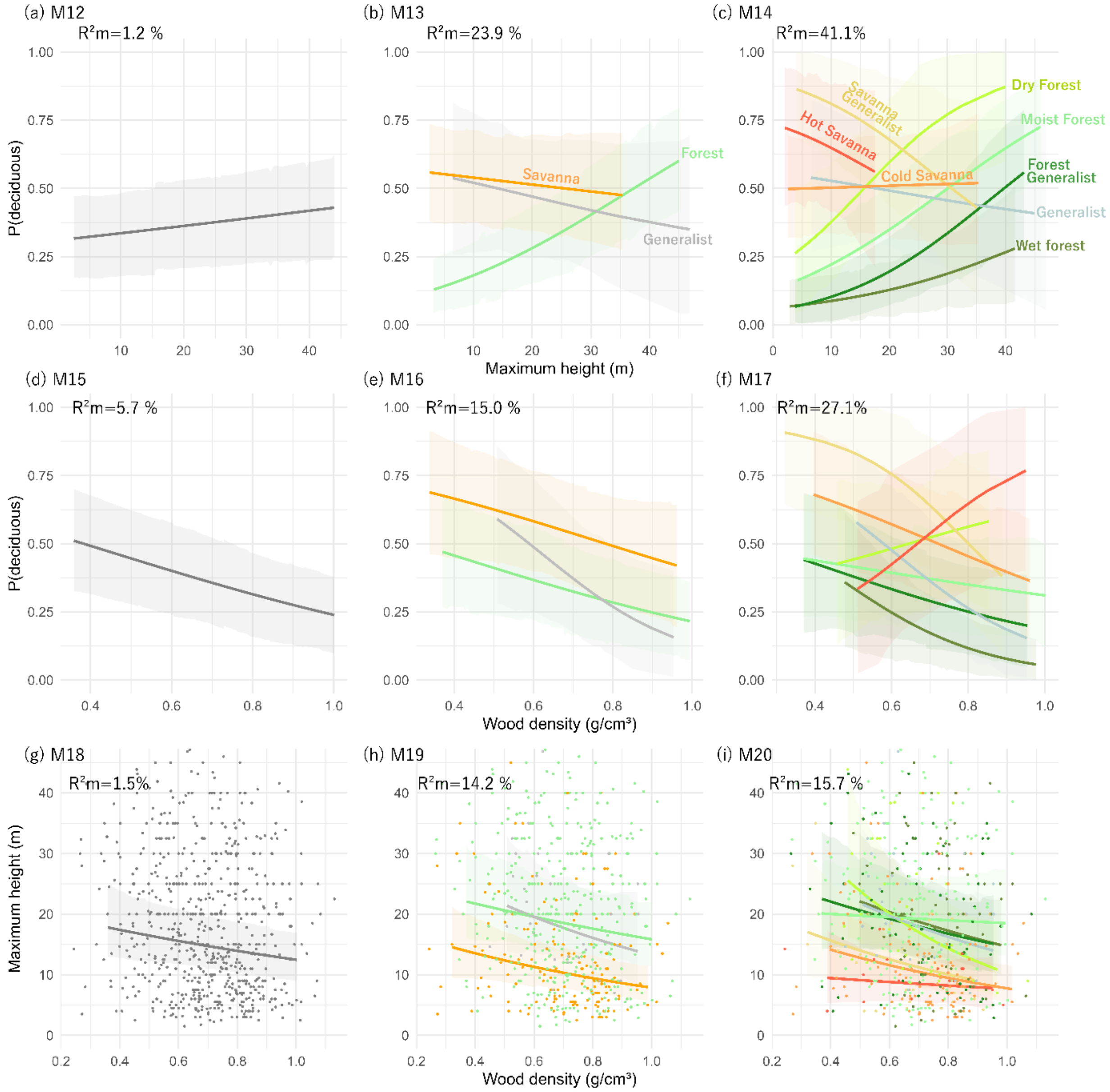

Figure 4 Prediction (without random effect) and confidence intervals of models testing the effect of maximum height (a, b, c) and wood density (d, e, f) on the probability to be deciduous (P(deciduous)), in general (a, d), then considering biomes (b, e) and phytoclimatic groups (c, f). Data, predictions, and confidence intervals of models testing the relationship between maximum height and wood density (g) and considering biomes (h) and phytoclimatic groups (i). The marginal variance R²m is given for each model.

Discussion

In this study, we offer new insights into the relationship between species climatic niche, traits, and phylogenetic relatedness in the tropical woody flora of Africa. Species within the same lineage tend to occupy similar climatic niches and share comparable attributes, with leaf habit being the most conserved trait. However, despite the strong phylogenetic signals identified, our findings also indicate that evolutionary changes, particularly within genera, significantly contribute to variations in both the climatic niche and traits. Climate alone was found to be a poor predictor of species leaf habit and our results emphasize the necessity of incorporating species maximum height or, to a lesser extent, wood density to enhance the accuracy of predictions. Our results also confirm that, in forest, the probability to be deciduous increases with water deficit, given the significant advantages of this drought avoidance strategy in drier environments. Furthermore, we demonstrated that the probability of a species to be deciduous increases with maximum height and inversely with wood density. We modelled the changes in species attributes based on their maximum height: from small understory species, which are more likely to be evergreen, have dense wood and are possibly more drought tolerant, to taller, light-wooded canopy species which are more likely to be deciduous and avoid drought.

The phylogenetic constraint on species climatic niche and traits

Our results for the African woody flora confirm the accumulating evidence of high phylogenetic signal in plants, both for the climatic niche and traits. We found that most of the variability in the species climatic niche (around 68% when considering biome affinity, 51% for phytoclimatic groups) is associated with phylogenetic relatedness, testifying to the tendency of related species to grow under similar climates. These results are in line with the high climatic niche conservatism previously found in plants across the global tropics (Crisp et al., 2009; Ringelberg et al., 2023 for Mimosoids) and in tropical Africa (Gorel et al., 2022). Regarding traits, leaf habit showed a high phylogenetic signal, with approximatively 70% of its variability related to phylogenetic relatedness. To date, our study represents the first quantitative assessment of the phylogenetic signal in the species leaf habit for the African flora. This result confirms that it is reasonable to use data observed at the genus or family level as a proxy of species leaf habit if this information is lacking. High phylogenetic signals have also been reported for maximum height (Feng et al., 2023; Liu et al., 2015 for Magnioliaceae), and to a lesser extent for wood density (Chave et al., 2006; Liu et al., 2015; Swenson & Enquist, 2007). The substantial phylogenetic signal we found for both the climatic niche and traits highlights that research in species phenology (Davies et al., 2013), maximum height and to a lesser extent wood density must take phylogeny into account because species cannot be treated as statistically independent.

Despite a strong phylogenetic signal, a notable proportion of the variability in the climatic niche and traits shows signs of rapid evolutionary changes induced by selection. These changes occurred both above the genus level (particularly for the climatic niche, the leaf habit, and the wood density) and within genera (particularly for the phytoclimatic group, the maximum height). We confirm a certain lability of the climatic niche, albeit relative, as it has already been demonstrated for particular woody genera, such as the iconic *Diospyro*s genus (White, 1978, 1988) or *Erythrophleum* (Gorel et al., 2019) which include both forest and savanna species. The approach was earlier extended to the tropical woody flora of Africa and niche lability was found to be widespread though niche conservatism dominates (Gorel et al., 2022). Similarly, while leaf habit is characterised by a high phylogenetic signal, a certain degree of lability has nevertheless been documented for certain clades, such as the Meliaceae family (Koenen et al., 2015) or the *Viburnum* genus (Edwards et al., 2017). The lability in leaf habit could be shared by many other lineages. The proof is that, despite we found a prevalence within families of one specific leaf habit reflecting high phylogenetic constraints, almost none of them consists exclusively of deciduous or evergreen species. Concerning wood density, a previous study in the Neotropics showed that around 30% of the variation was related to differences within genera (Chave et al., 2006) and we obtained a very close figure of 32%. It is worth noting that measurement inaccuracies for wood density, averaged from individuals of various sizes, may also artificially increase species variability. Indeed, both wood anatomy and density, is known to vary considerably depending on the tree size and age (Bastin et al., 2015; Beeckman, 2016; Doucet et al., 2022) and on the sampling position on the trunk (Kafuti et al., 2019). In general, it is important to recognize that our findings may be influenced by phenotypic plasticity or measurement errors (Housworth et al., 2004). Additionally, we cannot control the extent to which trait attributes are phylogenetically structured within genera, which could lead to an underestimation of the true phylogenetic signal. The forthcoming nuclear phylogenies will provide a more robust framework for re-evaluating our findings at the intrageneric level.

Trait response to climate

Our modelling framework allowed us to show that relying solely on climate was insufficient for accurate predictions of species leaf habit or maximum height. Indeed, despite the greater abundance of deciduous trees in savannas than in forests, evergreen and deciduous trees coexist in both biomes. This pattern suggests that both strategies, drought tolerance and drought avoidance, might be effective for coping with seasonal drought. However, our model predictions aligned with recognized trait variation across climates. For instance, the probability to be deciduous was notably lower for forest species compared to savanna species, consistent with earlier findings in northern and western African savannas (de Bie et al., 1998; Seghieri et al., 2012) and within the *Diospyros* genus (White, 1978). We found an increase in the probability to be deciduous with water deficit for forest species, in accordance with the variation of plot-level deciduousness across the Congo basin previously demonstrated (Réjou-Méchain et al., 2021). Species wood density appeared to be decoupled from climatic conditions, which aligns with earlier findings in the Neotropics (Chave et al., 2006; Poorter et al., 2019, the latter reported similar community-weighted mean wood density in wet and dry mature forests). Although these studies used basic wood density, and our results are based on oven-dry wood density, we remain confident that these two density values are comparable in terms of their responses to environment, because wood density values are highly correlated as shown for basic and 12% humidity (Vieilledent et al., 2018).

The leaf habit response to climate is mediated by species stature and wood density

Within the forest biome, the response of species leaf habit to climate became evident when considering covariations with maximum height or wood density, with a greater probability to be deciduous for tall species with slight wood and growing under greater Climatic Water Deficit. Our results are in line with previous findings showing that deciduous species tend to have lower wood density, an attribute associated with optimized resource acquisition (Markesteijn et al., 2011) and the attainment of greater heights (Anfodillo et al., 2006; Fajardo, 2022). In addition, lower wood density has been associated with higher hydraulic capacitance (Lachenbruch et al., 2011) which could effectively delay embolism formation and facilitate embolism recovery during brief episodes of water shortage when trees are still leafed. Small evergreen species shows opposite attributes, with dense wood which may reflect their higher tolerance to desiccation (Gorel et al., 2019; Liang et al., 2021; Markesteijn et al., 2011) and to shade (Kitajima & Poorter, 2010; Sterck et al., 2006). Although this trend is generally observed, some species and clades deviate from it. For instance, in the Irvingiaceae family, most species in our dataset are deciduous and reach significant heights, yet they have a higher wood density than expected based on our models (see Appendix 1 in SI). Furthermore, while this general trend is evident in all forest phytoclimatic groups (except for the dry forest when leaf habit is considered in relation to wood density), there are slight variations according to water deficit. Indeed, in the wet forest, where water availability is less restrictive, some tree species can be evergreen, have light wood, and be able to reach the canopy, as theorized in Oliveira *et al.* (2021). In moist forest characterized by drier and more seasonal climates, this combination of traits seems rather unlikely, as it considerably increases the risk of hydraulic failure (Hacke et al., 2022; McDowell et al., 2008; Olson et al., 2018). For savanna species, which are typically more deciduous and smaller than forest species, identifying a consistent pattern of trait co-variation across different climates remains challenging. In cold savannas, the probability to be deciduous was not correlated with maximum height but decline with wood density. This mirrors the trade-off observed in forest species and documented in savannas in China (Zhang et al., 2022), where species either mitigate drought stress through leaf shedding or withstand embolism with denser wood investment. Unlike forest species, however, adopting either strategy does not distinctly influence height. A particularly intriguing trend emerges among savanna generalists and hot savanna species: taller species are more likely to be evergreen. Additionally, in hot savannas and dry forests, the probability to be deciduous increases with wood density, suggesting a complementarity between leaf shedding strategies and high wood density investment. We currently lack clear ecological explanations for these counterintuitive patterns. Unlike in wet and moist forests, there is limited research on how leaf habit, maximum height, and wood density interact for drought adaptation in drier environments. Research in savannas has primarily focused on root densities, storage allocation patterns, and regrowth capacity (Sankaran, 2019 and references therein). Further investigations into morphological and physiological traits are essential to unravel these complexities and deepen our understanding of ecological strategies in drier environments.

To conclude, our study offers important insights into how phylogenetic constraints and climate shape species traits and their covariation across tropical Africa's woody flora. We recognize that large-scale trait data compilations may introduce some inaccuracies, such as approximations in maximum height or leaf habit reporting in floras. Additionally, our niche-based method may sometimes fail to fully capture the precise climatic conditions each species inhabits. However, given the scarcity of available data, we believe our effort represents one of the most comprehensive and feasible approaches for studying these large-scale ecological patterns, specifically for this flora. Large-scale comparisons of plant functional traits traditionally encompass specific leaf area, maximum height, seed mass (leaf-height-seed strategy scheme of Westoby, 1998), and wood density (Chave et al., 2009), and here we claim that for the tropical woody flora of Africa, considering information on leaf habit is equally crucial. Our current definitions of leaf habit, which rely on the dichotomy between deciduous and evergreen, may oversimplify the complex range of leaf phenology strategies reported for savanna species (e.g. de Bie et al., 1998), however, detailed information on leaf phenology remains scarce for the majority of species. The use of innovative tools such as phenocam (digital camera capturing time-lapse images of foliage, Brown et al., 2016) shows great potential in obtaining more refined data, while our results, derived from simple and readily accessible data, mark an initial step towards understanding the drought-related strategies employed by tropical trees.

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