



LETTER

Climatic niche lability but growth form conservatism in the African woody flora

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Abstract

Climatic niche evolution during the diversification of tropical plants has received little attention in Africa. To address this, we characterised the climatic niche of >4000 tropical African woody species, distinguishing two broad bioclimatic groups (forest vs. savanna) and six subgroups. We quantified niche conservatism *versus* lability at the genus level and for higher clades, using a molecular phylogeny of >800 genera. Although niche stasis at speciation is prevalent, numerous clades individually cover vast climatic spaces suggesting a general ease in transcending ecological limits, especially across bioclimatic subgroups. The forest biome was the main source of diversity, providing many lineages to savanna, but reverse shifts also occurred. We identified clades that diversified in savanna after shifts from forest. The forest-savanna transition was not consistently associated with a growth form change, though we found evolutionarily labile clades whose presence in forest or savanna is associated respectively with climbing or shrubby species diversification.

KEY WORDS

bioclimatic groups, forest, growth forms, large-scale niche evolution, niche lability, savanna, tropical Africa, woody species

INTRODUCTION

Phylogenetic niche conservatism refers to a pattern whereby lineages retain ancestral ecological traits (Harvey & Pagel, 1991). At a large scale, high levels of conservatism have been reported for plants (e.g., in the southern hemisphere, Crisp et al., 2009; for the succulent

biome, Ringelberg et al., 2020; and across the Americas, Segovia et al., 2020), demonstrating the prevalence of biome stasis at speciation and designating niche conservatism as a key factor structuring the distribution of plant diversity. Even within the moist tropical forest biome, independent phylogenetic reconstructions of the niche of tree lineages were strongly correlated

between continents, indicating a worldwide deep phylogenetic signal for the climatic niche (Hardy et al., 2012). However, many plant clades have transcended ecological barriers (Donoghue & Edwards, 2014), as illustrated by the multiple evolutions toward C4 photosynthesis in arid regions (over 45 times in 19 Angiosperm families, Sage, 2004) and the recurrent adaptation of some ancestrally tropical clades to frost and temperate climates (Preston & Sandve, 2013; Zanne et al., 2014). Large-scale niche evolution is certainly easier for some clades and for some ecological transitions, but there is still a lack of general knowledge about these evolutionary patterns and processes.

Biomes are the most widely used vegetation units for studying large-scale niche lability as biome shifts are viewed as major transitions entailing significant adaptations (Donoghue & Edwards, 2014). The premise behind the biome concept is that the environment imposes, selects and filters for vegetation attributes, producing global vegetation units that are similar in physiognomy and function (Moncrieff et al., 2016). It has been proposed that robust biome definition requires the identification of traits with adaptive value and that are easily measurable on many species in many sites (Shipley et al., 2016). However, trait-based biome delineation has been limited to a few traits, which may not entirely capture ecosystem structure and function (e.g. Conradi et al., 2020 using life forms in Africa). An alternative way is to group species that share similar environmental requirements, using ecological niche modelling (Broennimann et al., 2012), quantification of niche similarity (Warren et al., 2008) and statistically-driven clustering. Groups of species are predicted based on one simple overriding parameter, climatic niche similarity, which encompasses the wide range of strategies that allow plants to persist in particular conditions (Bilton et al., 2016). The divisions between such species groups (hereafter called ‘bioclimatic groups’) reflect significant ecological boundaries that have limited, and still limit, the distribution of some higher-level clades, but may be permeable to others through functional, and potentially clade-specific, adaptations.

Combined with exposure to contrasting habitats, the likelihood that a clade will successfully diversify across environmental boundaries depends on its ability to achieve different ecologically adaptive phenotypes (Donoghue & Edwards, 2014; Nürk et al., 2020). However, apart from some notable cases (e.g. Sage, 2004; Hearn, 2006; Simon & Pennington, 2012), little is known about the functional changes underlying niche evolution, particularly for woody clades in the tropics. Among many candidate traits, growth form lability (i.e. the propensity of the lineage to change growth form) could be a key innovation offering the ecological opportunity for adaptive diversification in forest, savanna and beyond (Rowe & Speck, 2005).

On the African continent and elsewhere, despite the prevalence of niche conservatism in plants (Crisp et al.,

2009; Linder et al., 2012; Segovia et al., 2020), many clades have transcended major ecological barriers, such as the forest-savanna boundary (see White, 1978 for *Diospyros*; Gorel et al., 2019 for *Erythrophleum* and references therein), but the direction, timing, functional trait association and distribution of such shifts over plant phylogeny have not been characterised at the scale of a whole flora. Here, we determined the climatic niche lability of the African tropical woody flora. We developed an approach to quantify niche conservatism *versus* lability, determining the climatic limits that constrain most clades and identifying which clades transcend these limits. Genus-level phylogenies were used to infer the timing and origin of the woody flora in the major bioclimatic groups (i.e. the forest and savanna biomes). We delineated bioclimatic groups based on species niche similarity by using published occurrence data in conjunction with climatic layers to model the climatic niche of >4000 woody species. We restricted our analysis to woody plants to grasp the common ecological and adaptive constraints of clades that share this life history strategy. We specifically ask the following questions.

How labile is climatic niche in the tropical woody flora? Numerous genera and families are expected to cover multiple bioclimatic groups at present and, from the Eocene, multiple shifts between the forest and savanna biomes are expected above the genus level. We specifically expected an increasing proportion of forest to savanna biome shifts given the general trend of increasing aridification throughout the Cenozoic (Kissling et al., 2012).

How does niche lability vary across ecological boundaries and clades? More transitions are expected between climatically similar bioclimatic groups, since such transitions require less functional change. We expected niche lability to be uneven across clades because the intrinsic propensity of a lineage to evolve towards contrasting climate may require clade-specific adaptations. Because past niche shifts could increase the diversification rate, a positive association between clade richness and niche lability is also expected.

Is niche lability between the bioclimatic groups (forest vs. savanna) associated with growth form lability? Labile genera and families are expected to present more climbing species in forest and more shrubby species in savanna.

MATERIAL AND METHODS

Species occurrence and climatic layers

Occurrence data of native woody species were extracted from the RAINBIO database, which contains 593,861 georeferenced occurrences derived from herbarium vouchers collected across tropical Africa between 1782 and 2015, and representing 25,356 plant species (Dauby

et al., 2016). The area covered from 20°N to 35°S is broadly defined as sub-Saharan Africa excluding South Africa and Madagascar. Most of the species (91%) have been scored for growth form (tree, shrub, shrublet, herb, climber, liana, vine, epiphyte and parasitic). Occurrences of exotic/cultivated species or specimens collected in botanical gardens or equivalent were removed as well as occurrences without identification down to the species level and with poor georeferencing accuracy ('accuracy' ≤ 3). Since we were interested in woody species, we considered genera containing species scored as 'tree', 'shrub', 'shrublet', 'vine', 'climber' and 'liana'. For genera with only species assigned to 'climber' and 'vine' forms, flora and herbarium specimen were consulted to determine woodiness. The woody species lists from Fayolle et al. (2014, 2019) for forest and savanna sites, respectively, were also included, resulting in a combined dataset containing the occurrences of 8232 species belonging to 1292 genera and 169 families (329,381 occurrences). The taxonomy followed the original RAINBIO database (Dauby et al., 2016) with the exception of the African Acacias that were assigned to either *Vachellia* or *Senegalia* following Kyalangalilwa et al. (2013).

The bioclimatic variables of the CMCC-BioClimInd data set (Noce et al., 2020) were assembled for continental Africa. We used all variables, apart from the Modified Kira coldness index (Bio25) and the Ombrothermic index of summer of the previous month (Bio33), both of little interest in the tropics. The maximum climatological water deficit (CWD) was extracted from Chave et al. (2014). All variables were scaled to a 2.5 arc minute grid resolution.

Niche modelling

To select the most appropriate climatic space to model species niches, we first performed a principal component analysis (PCA) using the pixel values of the climatic layers for the whole African continent. In the space defined by the first two axes, we projected the scores of the pixels with at least one species occurrence and estimated kernel densities. For subsequent niche modelling, the climatic background corresponds to the values of the principal components within the 99% kernel densities, to avoid bias due to species occupying extreme environments while keeping the maximum number of species. In addition, we kept only species with at least 90% of occupied pixels inside the selected climatic background to avoid bias due to incomplete coverage of their distribution (7928 species, 1260 genera, 167 families).

The niche of each species was then delineated within the climatic space defined by the first two axes of the PCA calibrated with the selected climatic background (Broennimann et al., 2012). The two principal components correspond to two main environmental gradients (Figure S1). A mean temperature gradient (44.4%

variance explained) opposed warmer areas with higher potential evapotranspiration (positive scores) to cooler areas (negative scores) and a rainfall/temperature seasonality gradient (34.6% variance explained) opposed drier areas with high temperature seasonality (positive scores) to wetter and more isothermal areas (negative scores). PCA scores were obtained for all occurrences and at this stage, we retained the species with at least seven climatically unique occurrences (4154 species; 960 genera; 138 families, totalling 288,412 occurrences). For each species, the PCA scores of the occurrences were projected onto a grid of cells bounded by the minimum and maximum scores in the climatic space. The species niche was defined as the smoothed density of occurrences in each cell of the grid estimated using a kernel density function.

Species clustering

To group species according to their climatic niche, we first created a niche dissimilarity matrix. To quantify niche overlap among all pairs of species, we used the Hellinger's I statistic (Warren et al., 2008). The overlap varies between 0 (no overlap) and 1 (complete overlap, identical niches). The corresponding dissimilarity matrix (1-I) was built containing the value of niche dissimilarity for all pairs of species retained (4154 species \times 4154 species). A non-metric multidimensional scaling (NMDS, results not shown) was used to visualise the niche dissimilarity into a two-dimensional space and at this stage, we excluded from the dataset 12 species whose distributions were centred in the Kalahari desert (at the edge of the RAINBIO geographical coverage). A hierarchical clustering approach was used for grouping the 4142 retained species (956 genera, and 138 families) occupying similar climates, whether or not they are found in the same geographical area. We used Ward's algorithm for creating the dendrogram representing niche (dis-)similarity among species. A silhouette analysis was used to choose the optimal number of clusters (Figure S2) and we retained two and six bioclimatic groups and subgroups, respectively, that were mapped in the climatic and geographic spaces by calculating for each pixel the proportion of species assigned to one bioclimatic (sub)group. Only species with a positive silhouette width, that is, well assigned to the (sub)group, not transitional, were used ($n = 3997$ species for the two groups, $n = 3476$ for the six subgroups). A resolution of 75 arc minute was used for the geographical space.

Ancestral biome reconstruction

We developed a genus-level phylogeny following Segovia et al. (2020) and Sanchez-Martinez et al. (2020) in which the species were attached to their respective genus as

polytomies (Figure S10). We did not consider large-scale phylogenies resolved to the species level because they are still largely based on plastid markers and their topologies are not reliable for many genera due to recurrent chloroplast captures (see references in SI). The final dataset consisted of 813 genera (85% of coverage) and 3639 species mapped onto the time-calibrated phylogeny. Ancestral biomes (i.e. the major bioclimatic groups, forest vs. savanna) were reconstructed with generalised Markov models, without and with hidden states (Boyko & Beaulieu, 2021). The complete model selection procedure is given in SI as well as the phylogeny with marginal reconstructions (Figure S10). We focused on a single rate (ER) model across the phylogeny. At each node, the most likely biome state was estimated. The ER model predictions have been compared with those of the AIC-supported *ARD/ARD* model (Tables S5 and S6, Figure S9).

Data analyses

To estimate niche lability in the African woody flora, we first identified polytypic and conserved genera and families, that is, with all their species currently in the same bioclimatic (sub)group, and labile genera and families, that is, with their species currently split into different bioclimatic (sub)groups. In addition, we used the most likely biome states reconstructed across the phylogeny to estimate the proportion of speciation events involving a biome shift since 50 Ma (Eocene). Above the genus level and in 10 Ma bins, we computed the proportion of speciation events associated or not with a directional shift between the forest and the savanna biomes, considering the midpoint of branches as the age of the speciation events. Within genera, because the phylogeny is not resolved, only the minimum number of directional shifts was estimated, that is, just one shift in labile genera.

To examine how niche lability varies across ecological boundaries, the ease of transition between all pairs of bioclimatic (sub)groups was inferred by their current taxonomic similarity. We computed the Simpson similarity index at genus and family levels (the number of shared genera/families divided by the number of genera/families occurring in the smaller sample). The link between the taxonomic similarity of bioclimatic (sub)groups and their environmental and geographical distances (estimated as the Hellinger's I overlap of cluster projections) was tested using Spearman correlation tests.

To examine how niche lability varies across clades, we first identified the most ecologically diverse genera and families at present and evaluated how species richness in genera and families varied with niche lability. To avoid sampling bias, we used sample-based rarefaction to estimate the number of subgroups occupied by each genus and family when resampling six species, and tested whether it increased with total species richness

(using Spearman correlation test), as expected if past niche shifts tend to increase the diversification rate. We also tested the effect of clade ages. Then, we further investigated shifts between the forest and savanna biomes by identifying clades which currently have more forest (or savanna) species than expected by chance using an exact test of goodness of fit with an assumed probability of 0.70 for forest and 0.30 for savanna (i.e. matching the proportion of forest and savanna species in the data set). Based on the ancestral biome reconstruction since 50 Ma, we estimated the proportion and timing of shifts for each order and family (with more than three genera).

To test whether transitions between the forest and savanna biomes are associated with a change in growth form, we estimated the effects of biome and genus/family on growth form (shrub vs. tree vs. climber, the latter including species scored as 'vine', 'climber' and 'liana') based on the estimation of variance components of fitted binomial mixed-effect models where genus/family were the random effects, following Nakagawa et al. (2017). In addition, we used Fisher's exact test for count data separately for each labile genus and family, that is, with species both in forest and savanna, to test the independence between growth forms and biomes.

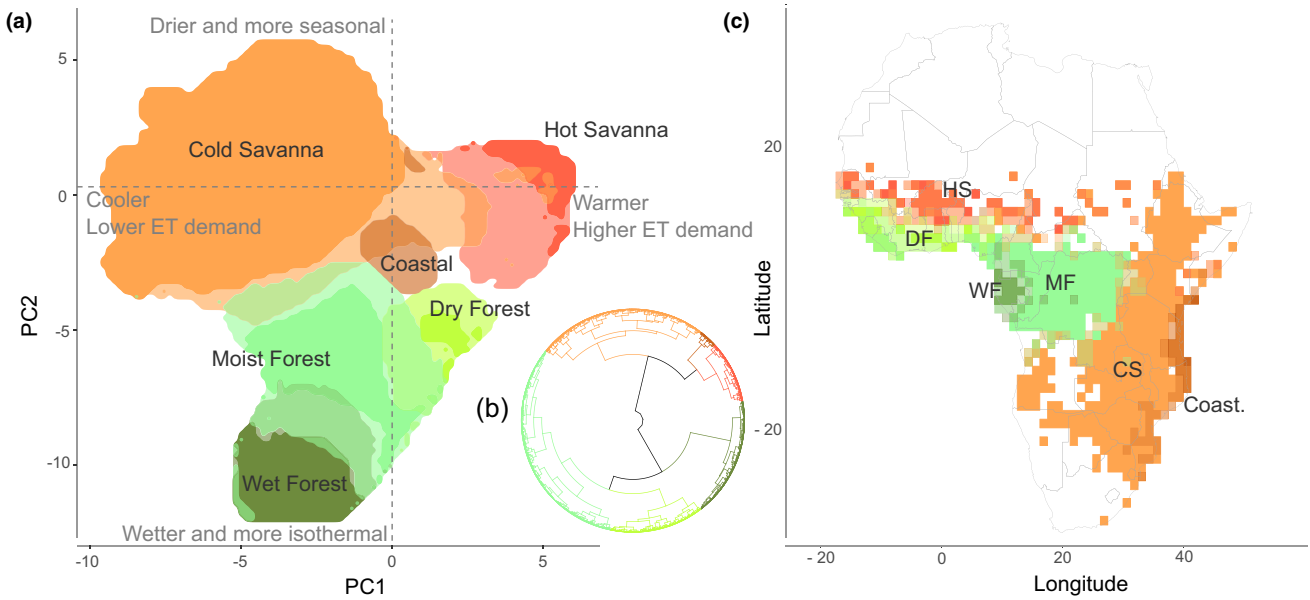
All analyses were performed in the R Statistical Environment (R Core Team, 2019) using the 'ade4' (Thioulouse et al., 2018) and 'vegan' (Oksanen et al., 2007) packages, respectively, for the PCA and NMDS ordinations, the 'ecospat' package (Di Cola et al., 2017) for niche modelling and overlap (Hellinger's I statistic), the 'stat' package for species clustering with the Ward's algorithm, the 'rptR' package (Stoffel et al., 2017) for computing the proportion of variance in growth form explained by random and fixed factors by performing bootstrapping 100 times, and the 'corHMM' package (Boyko & Beaulieu, 2021) for ancestral biome reconstruction.

RESULTS

Climatic niches

The species were divided into two major bioclimatic groups (Figure 1) differentiated along the rainfall/temperature seasonality gradient. These two bioclimatic groups closely match the forest and the savanna biomes as shown by earlier maps (Figure S5a,b) and by the proportion of species assigned to each bioclimatic group in locations where in situ habitat is known (Figure S5d). The first major bioclimatic group, that is, the forest biome, was divided into three subgroups, whereas the second major bioclimatic group, that is, the savanna biome, was composed of two large savanna subgroups. A third smaller subgroup found along the Indian Ocean coastal belt (Figure 1a), hereafter referred as the 'Coastal' subgroup, was treated separately because it is a mosaic of forest and savanna. See in SI the distribution of the

Bioclimatic (sub)groups



Similarity in taxonomic composition

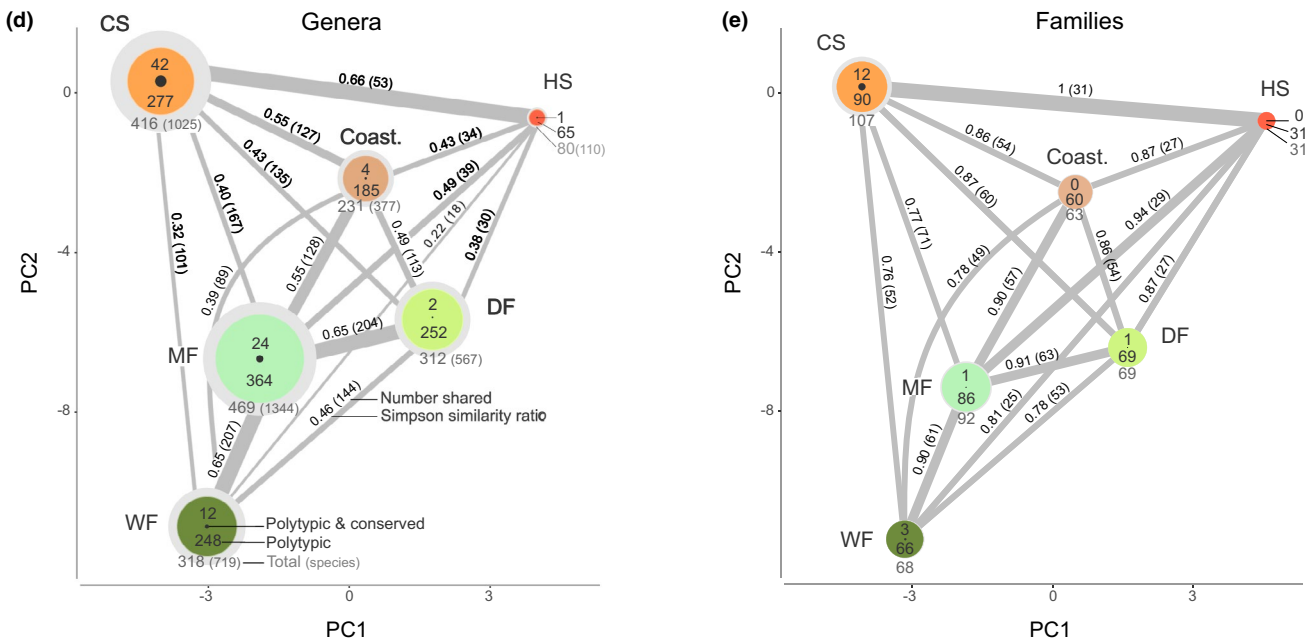


FIGURE 1 Bioclimatic groups (biomes) and subgroups and similarity in taxonomic composition. Based on the dendrogram derived from pairwise species niche similarity (b), the species were divided into two broad bioclimatic groups, closely representing the dichotomy between species associated to the forest (in green) and to the savanna (orange and red) biomes. Further divisions resulted in six subgroups, three forest subgroups (the ‘West Forest’ (WF) in dark green, the ‘Moist Forest’ (MF) in pale green and the ‘Dry Forest’ (DF) in yellow green), two savanna subgroups (the ‘Cold Savanna’ (CS) in orange, the ‘Hot Savanna’ (HS) in red) and one ‘Coastal’ subgroup (‘Coast’ in brown). The distribution of the subgroups is shown in ordinated climatic space (a) and in geographic space (c). Solid colours correspond to areas where more than 50% of the species present in the pixel were assigned to the corresponding cluster. The pixels coloured with partial transparency correspond to areas where more than 25%, but less than 50% of the species present in the pixel were assigned to the cluster. Between the subgroups, the similarity in taxonomic composition, and thus niche lability, was measured by the Simpson similarity for genera (d) and families (e). Each circle corresponds to one subgroup, positioned based on its centroid in the climate space. Outer grey circles show the total number of genera (or families in b) in the subgroup and the number of species in brackets. Inner circles show the number of polytypic (bottom) and conserved (top) genera (or families in e). The connecting lines and the associated numbers correspond to the Simpson's similarity index calculated for each pair of subgroups, with the number of shared genera (or families in e) in brackets

bioclimatic groups in climatic and geographic space (Figures S3 and S4), as well as the contributions of the climatic variables to the bioclimatic groups' delimitation (Table S1).

The forest biome occupied the wettest and more isothermal areas (Figure 1a) and its distribution extended from West to Central Africa (Figure 1c). This hyperdiverse biome included 2630 species from 673 genera and 104 families. Of these, 207 genera and 18 families were polytypic and conserved (i.e. with all their species in the forest biome). The most diverse among the conserved genera and families were, respectively, *Gilbertiodendron* (Fabaceae, 20 species) and Lecythidaceae (24 species). The 'Wet Forest' subgroup was typical of the climatic conditions encountered in Gabon (Figure 1c). The 'Moist Forest', the most diverse and conserved of the 'Forest' subgroups (Figure 1d,e), occupied a wider climatic and geographical area, both in West and Central Africa (Figure 1a,c). Finally, the species of the 'Dry Forest' subgroup were associated with the drier and warmer conditions of West Africa, over an area that largely overlapped the area occupied by the 'Moist Forest' but extended further north (Figure 1c).

The savanna biome occupied the driest areas and a wide range of temperatures, from the coldest to the hottest regions (Figure 1a). Species were found in Eastern, Western and Southern Africa (Figure 1c). This biome was less diverse in terms of woody species than the 'Forest' group, comprising 1135 species in 443 genera and 107 families. Of these, 69 genera and 14 families were polytypic and conserved, the most diversified being *Commiphora* (Burseraceae, 22 species) and Proteaceae (7 species). The 'Cold Savanna', the most diverse and conserved of the 'Savanna' subgroups (Figure 1d,e), had a very wide climatic breadth, composed of species present in the coldest and in the most arid conditions in Eastern and Southern Africa. The 'Hot Savanna' subgroup occupied the warmest and driest conditions in West Africa (Figure 1a,c).

The 'Coastal' subgroup was found in the Indian Ocean coastal belt. Although associated with a savanna-prone climate, the vegetation actually is a forest-savanna mosaic partly driven by complex topography (Burgess et al., 1998), which is not captured in our analysis due to the coarse resolution we used. This group showed little evidence for conservatism (Figure 1d,e), with no conserved

families and very few genera, the most diverse being *Hilsenbergia* (Boraginaceae, three species).

Niche lability across time

Considering that 84% of the polytypic genera ($n = 436$) and 84% of the polytypic families ($n = 94$) had species in at least two bioclimatic subgroups, niche lability can be considered common. Likewise, 43% of the polytypic genera ($n = 210$) and 70% of the polytypic families ($n = 76$) had species in both the forest and savanna biomes. Since 50 Ma at supra-genus level, the ER model predicted biome shifts for 7% of the 917 speciation events, the majority being from forest to savanna (74% of shifts, Figure 2, Table S2). The forest biome was conserved in 75% of the events and the savanna biome in 18%. Although the number of speciation events increase since 50 Ma, the proportion of shifts remains relatively constant (Figure 2c). Forest was the most likely ancestral biome of the majority of genera occurring both in forest and savanna (73%). Similar results were obtained with an ARD/ARD model (Tables S5 and S6, Figure S9).

Niche lability across bioclimatic groups

The ease of transition between all pairs of bioclimatic (sub)groups was inferred by their current taxonomic similarity. Between the forest and the savanna biomes, the taxonomic similarity (measured with the Simpson index) was 0.47 for genera and 0.73 for families. Between subgroups, similarity ranged from 0.22 to 0.65 for genera (Figure 1d) and similarity increased with environmental proximity ($r_s = 0.79$) and, to a lesser extent, with current geographic proximity ($r_s = 0.65$). These relationships were weaker for families ($r_s = 0.44$ and 0.46 for environmental and geographic overlap, respectively) indicating that most families were found in the subgroups, regardless of the current geographical and environmental proximity (Figure 1e). The highest similarity was found between the 'Cold Savanna' and the 'Hot Savanna' subgroups. The 'Coastal' subgroup had an intermediate composition between forest and savanna, sharing many genera and families both with the 'Moist Forest' and with the 'Cold savanna' (Figure 1d,e).

FIGURE 2 Biome lability across time. (a) Ancestral biome reconstruction for woody Angiosperms. The tree was coloured according to the most likely states of nodes (green: forest, orange: savanna), and some ancestral nodes corresponding to taxonomic orders were highlighted. The complete phylogenetic tree for angiosperms and the few gymnosperms we studied is given in SI (Figure S10). (b) The current biome specialisation (more species in one biome than expected by chance) and conservation are given for genus, family and orders with the same colour coding as Figure 4: orange and pale green clades have more species, respectively, in savanna and forest, than expected by chance (hereafter called savanna- and forest-specialised clades). Red and dark green clades are totally conserved, respectively, in savanna and forest. Blue clades have a forest-savanna species distribution that do not differ significantly from that expected by chance. (c) Timing of speciation events and shifts since 50 Ma for all lineages and four highly diversified orders. The bars represent the number of speciation events on our phylogeny (left axis) and the line represents the percentage of speciation events associated with biome shifts (right axis)

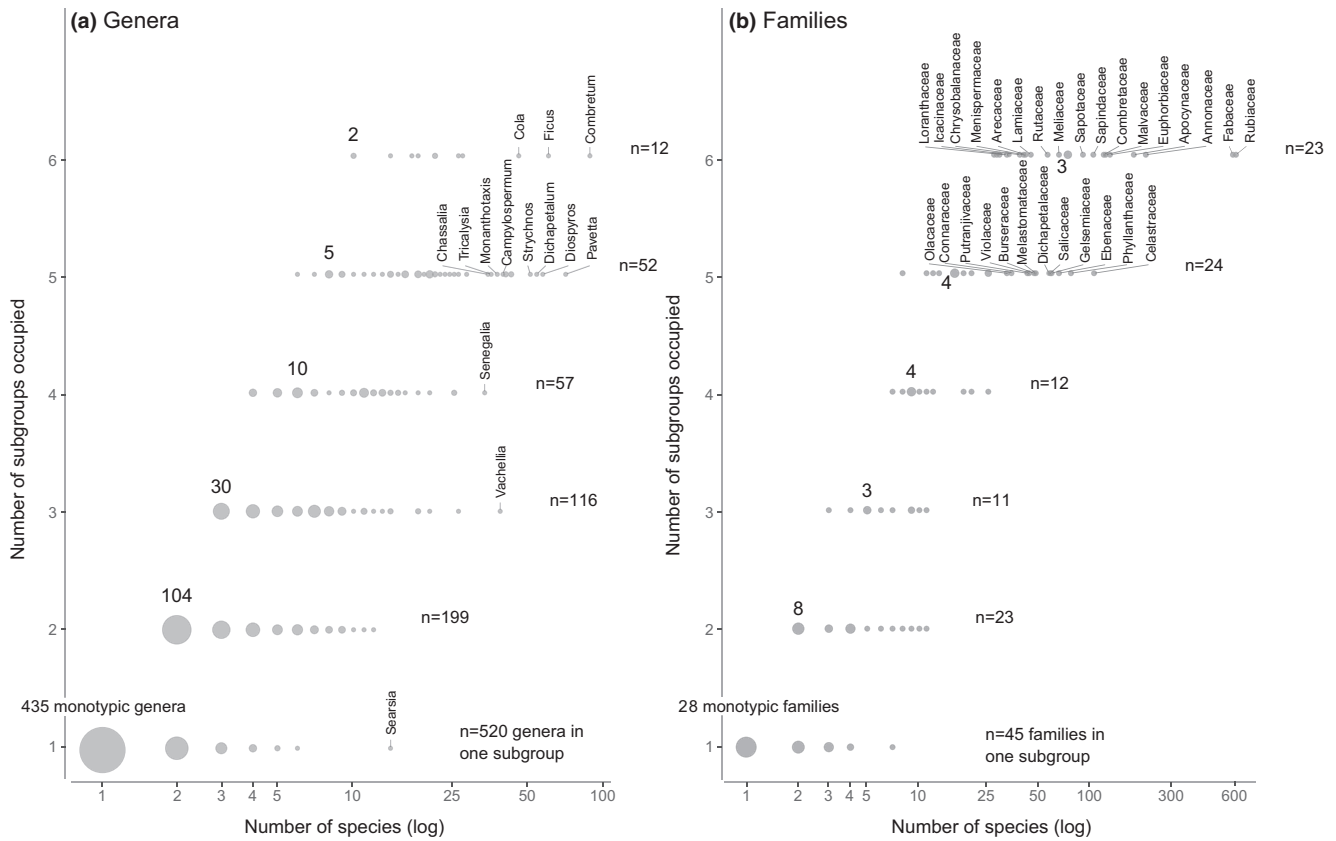


FIGURE 3 Number of bioclimatic subgroups occupied by genera (a) and families (b) in relation to their species richness (\log_{10}). The size of the dots is proportional to the number of genera (or families in b) for each combination and the actual number is given next to a few dots. The total number of genera (or families in b) occupying from one to six different subgroups are given on the right. The name of the most diversified genera (or families in b) is shown

richness (Figure S6), but no significant correlation was detected with genus (-family) age. Twelve genera and twenty-three families were found to be so ecologically labile that they have species across all six bioclimatic subgroups. This is particularly true for the hyperdiverse *Combretum* ($n = 86$ species), *Ficus* ($n = 59$) and *Cola* ($n = 45$) genera (Figure 3a), and for the hyperdiverse *Rubiaceae* and *Fabaceae* families (Figure 3b).

Current patterns of biome conservatism and specialisation (Figure 4) were related to contrasting evolutionary histories and lability across clades (Figure 2, Table S2). The majority of clades currently have more species in the forest than in the savanna biome (Figure 4), as the result of very high forest conservatism since 50 Ma (Figure 2a,b). The Magnoliales (including the *Annonaceae* family), with a large majority of speciation events within the forest biome (97%), was one of the most forest conserved but hyperdiversified orders (Figure 2). The proportion of species in forest versus savanna for most clades did not differ significantly from that expected by chance (90% of genera, 70% of families, 60% of orders, $p \leq 0.05$), although we found several savanna-specialised families and orders (Figures 2b and 4). Some of them, such as the Lamiales, displayed high levels of savanna conservatism at speciation events (80%) but also reverse shifts from savanna to forest (17%). Others, such as the Fabales (and *Fabaceae*), while having high forest

conservatism (80% of the speciation events), have shifted many times from forest to savanna (10%), which explains the current presence of many savanna-specialised lineages (Figure 2b). The Malpighiales, currently forest-specialised (Figure 2b), was also characterised by forest conservatism (80% speciation events), but showed lower levels of shifts, mostly from forest to savanna (5%).

Growth form lability

The forest and the savanna biomes were both half composed of tree species. Proportionally, the forest biome was richer in climbers than the savanna biome (26% vs. 8%, respectively), and the savanna biome was richer in shrubs (40% vs. 23%, respectively). Only half of the labile genera presented multiple growth forms, and rarely all three forms (10%). For labile families, change in growth form was more frequent (84%). Using the complete dataset and binomial mixed models, we did not detect significant ecological convergence in growth forms, but instead evidence for high conservatism at the genus level and, to a lesser extent, at the family level (Table 1). Conservatism at genus level was particularly strong for the climber growth form. Considering each labile genus and family separately, forest-savanna transitions were significantly associated with changes in

the distribution of growth forms for seven genera and 12 families (Fisher's test $p < 0.05$, names given in Figure 5), with significantly more climbers in the forest biome ($n = 5$ genera, $n = 8$ families) and more shrubs in the savanna biome ($n = 5$ genera, $n = 9$ families).

DISCUSSION

Climatic niches across the African tropical woody flora

In this study, we clustered 4142 woody species of tropical Africa according to their climatic niche similarity and the first division we obtained corresponds to the forest and savanna biomes. This result demonstrates that grouping species that share similar environmental requirements is a good alternative to using traits to approximate a common response to environment, although we recognise that forests and savannas can co-exist under a wide range of climates (Staver et al., 2011), where they can be alternative stable states maintained by feedbacks between tree cover and fire. Our method has a clear advantage in delineating meaningful groups within biomes, especially for forests, where differences in structure and function are subtle and not always easy to detect by remote sensing. We also identified six different subgroups, which represent the main climatic boundaries within biomes. The subgroups are distributed, respectively, along a precipitation/temperature seasonality gradient and a mean temperature gradient, two gradients strongly associated with variation in woody species composition (Fayolle et al., 2014, 2019). The 'Dry Forest' subgroup supports the existence of a flora adapted to seasonal drought stress in West Africa (Swaine, 1992). Within savanna, the 'Hot' and the 'Cold Savanna' subgroups corresponds to the floristic turnover associated with the steep change in altitude and temperature (Fayolle et al., 2019). The 'Cold Savanna' encompasses floristic heterogeneity (Linder et al., 2012), which is certainly not purely determined by climate but related to other environmental factors (e.g. soils, fire and herbivory).

Niche lability

As previously demonstrated for plants in the Southern Hemisphere (Crisp et al., 2009), biome stasis at speciation is prevalent (93% of speciation events since 50 Ma in this study). However, we identified numerous clades, which cover a vast climatic space and occur in multiple bioclimatic groups at present. A current forest-savanna partition has been detected for 40% of the polytypic woody genera studied, a figure that rises to over 80% when considering subgroup divisions within biomes. Pending the creation of a robust species-level phylogeny for African woody plants, our results already provide simple evidence of the ease to transcend major

ecological boundaries for many woody clades in tropical Africa. As previously demonstrated for the Neotropics (Antonelli et al., 2018), the forest biome appears to be the major source of diversity since we found a predominance of shifts from forest to savanna (73% of shifts since the Eocene), but reverse shifts from savanna to forest also occurred (e.g. in the Lamiales order). Our results did not confirm the hypothesis of an increasing proportion of forest to savanna biome shifts with time since the Eocene, but this hypothesis will need to be reassessed when a well-resolved phylogeny at the species level based on nuclear DNA sequences becomes available.

It is worth noting that ignoring herbaceous taxa might bias the assessments of shared taxa among bioclimatic groups, even up to the forest-savanna crossover, and niche conservatism is undoubtedly overestimated, at least for clades that also contain herbaceous species. For the ancestral biome reconstruction, focusing on only woody taxa leaves gaps in the study that are important, but we do not consider them to be fatal. In flowering plants, clades of non-woody species generally derive from woody ancestors (Doyle, 2012), then the evolution of woody species is little influenced by the evolution of related non-woody species. In addition, even in diverse clades that have a large proportion of woody and herbaceous plants, there are only few actual transitions from woody to herbaceous, for example, nearly all truly herbaceous species (e.g. not geoxyles) in the Fabaceae are restricted to one clade (in the Papilionoideae subfamily). However, we recognise that evolutionary reversals from herbaceous lineages to new woody species, as identified on islands (Hooft van Huysduynen et al., 2021), could obscure the ancestral biome reconstruction.

Niche lability was more frequent between climatically close subgroups since such shifts presumably require less functional change. Nevertheless, even the most climatically distant subgroups (i.e. 'Wet Forest' and 'Hot Savanna') share a significant number of genera and families, demonstrating that even very dissimilar regions, in terms of environment and biota, are highly evolutionarily interconnected. The high level of shifts between currently geographically remote but ecologically similar regions can be a signal of long distance dispersal with niche conservatism (Gagnon et al., 2019) but is more likely a signal of past connection. For instance, the 'Coastal' and the 'Moist Forest' subgroups, which shared a greater number of genera than would be predicted from their modern distribution, are associated with a long history of (re)connections (Couvreur et al., 2011). In the Indian Ocean Coastal Belt, the current climate in higher elevation areas has allowed the persistence of a forest flora, vicariant to the one of the Guineo-Congolian Region, while the lowlands have a climate favourable to a savanna flora (Burgess et al., 1998), related to that of the 'Cold Savanna'.

The extent of niche lability is uneven across clades, and we have shown that the richest genera (and

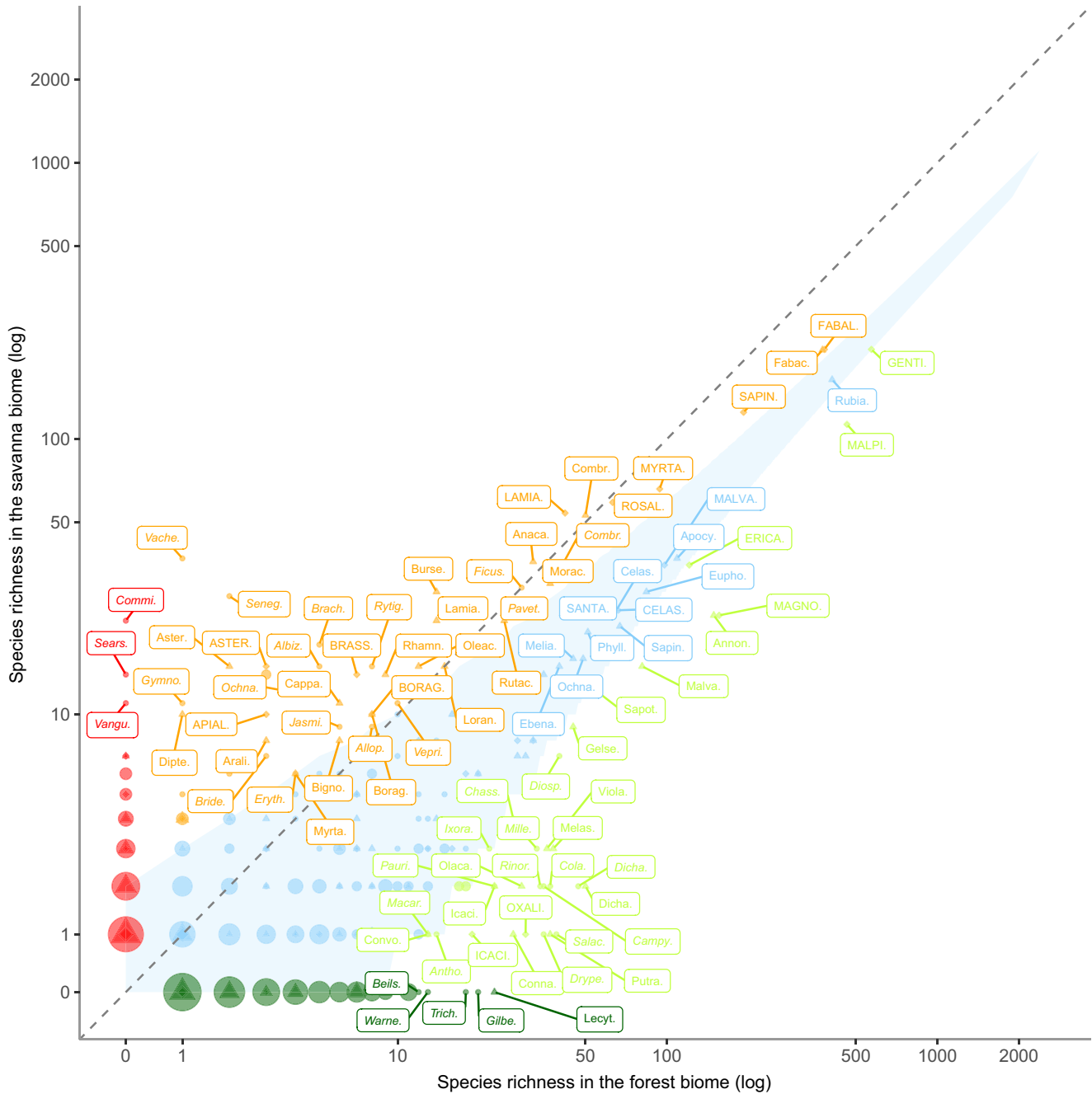


FIGURE 4 Species richness in the savanna biome compared with species richness in the forest biome for genera (dots, names in lower case and italics), families (triangle, names in lower case) and orders (diamond, names in upper case). The size of the symbols is proportional to the number of genera, families or orders and the names of the most diverse genera, families and orders are shown. The solid line represents the null 70:30 ratio: the number of forest versus savanna species as expected by chance, that is, following the proportion of species in forest and savanna in the whole dataset. The blue shaded area corresponds to values that do not differ significantly from that expected by chance. Orange and pale green clades have more species, respectively in savanna and forest, than expected by chance (i.e. savanna- and forest-specialised clades). Red and dark green clades are totally conserved, respectively, in savanna and forest. The dotted lines represent the 1:1 ratio

families) are generally the most ecologically diverse (apart from *Searsia*), a pattern robust even after taking into account sampling bias. As the age of the clades does not explain these differences, this result could be evidence of contrasting abilities to evolve and diversify in multiple environments. The ancestral character of the forest biome combined with a high level of conservatism explains the current higher species richness in

the forest biome for a majority of clades, as has been reported before (Eiserhardt et al., 2017). Nevertheless, we highlighted some clades, such as the Fabaceae, that have been particularly successful at diversifying in drier conditions after multiple shifts from forest and currently hold multiple savanna-specialist lineages. We also identify clades (e.g. Lamiales, Asterales), which are highly specialised to forest or savanna, with a

TABLE 1 Variance explained by fixed and random effects for models testing the relative effects of evolutionary convergence (savanna vs. forest biome, as fixed effect) and phylogenetic conservatism (family and genus as random effects) on growth forms: tree, shrub and climber

Models	Fixed variance (%)	Random variance (%)	Residual variance (%)
Tree ~ biome + (1 family)	0.01	52.30	47.69
Tree ~ biome + (1 genus)	0.06	71.52	28.42
Shrub ~ biome + (1 family)	3.01	21.25	75.74
Shrub ~ biome + (1 genus)	3.09	53.52	43.39
Climber ~ biome + (1 family)	2.80	63.23	33.97
Climber ~ biome + (1 genus)	0.58	97.80	1.62

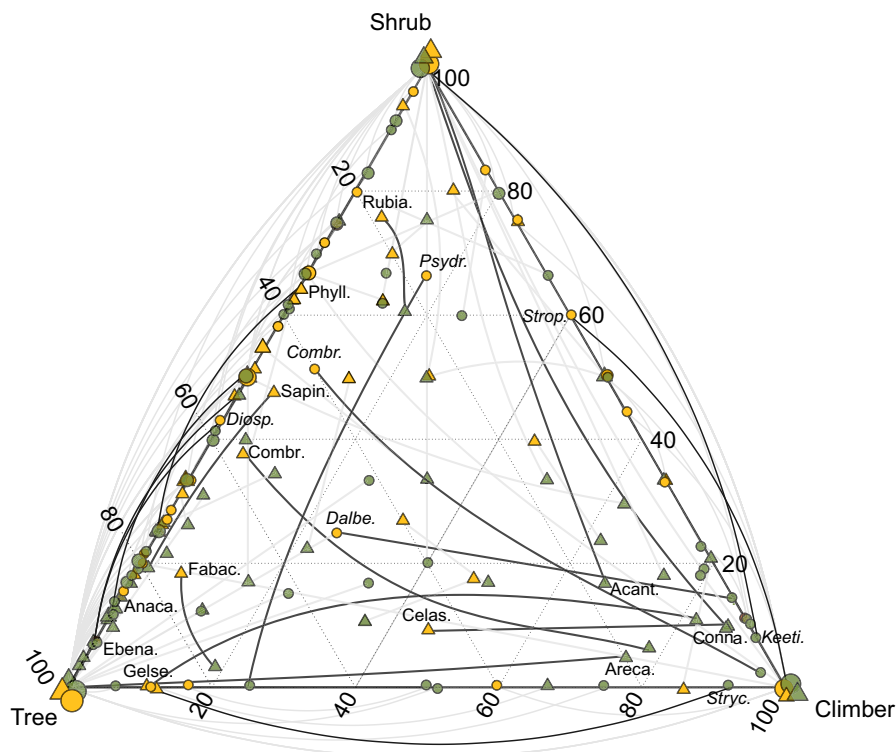


FIGURE 5 For each labile genus (dots, name in italic) and family (triangles), the percentage of trees, shrubs and climbers in the forest biome (green symbols) and in the savanna biome (orange symbols). The size of the symbols reflects the number of genera or families with the same values. The lines connect the two symbols for each genus or family and indicate the forest-savanna shifts in growth forms. The names of the genera ($n = 7$) and families ($n = 12$) having a significant change in the distribution of growth forms across the two biomes (according to the Fisher test, $p \leq 0.05$) are given with the line coloured black. Abbreviations for genera: *Combr.*: *Combretum*, *Dalbe.*: *Dalbergia*, *Diosp.*: *Diospyros*, *Keeti.*: *Keetia*, *Psydr.*: *Psydrax*, *Strop.*: *Strophanthus*, *Stryc.*: *Strychnos*. Families: *Acant.*: *Acanthaceae*, *Anaca.*: *Anacardiaceae*, *Areca.*: *Areaceae*, *Celas.*: *Celastraceae*, *Combr.*: *Combretaceae*, *Conna.*: *Connaraceae*, *Ebena.*: *Ebenaceae*, *Fabac.*: *Fabaceae*, *Gelse.*: *Gelsemiaceae*, *Phyll.*: *Phyllanthaceae*, *Rubia.*: *Rubiaceae*, *Sapin.*: *Sapindaceae*

particularly high biome stasis during speciation since the Eocene. For savanna-specialised clades, diversification into African savannas may have been preceded by intercontinental migrations with niche conservatism (Panero & Crozier, 2016 for the Asteraceae). The best way to explore the diversification of the flora would come from well-resolved species-level phylogenies, but we simply do not have enough of them for the African flora. However, we show that combining a taxonomic approach, that is, dissecting the current distribution of clades, with genus-level phylogenetic approach to infer the evolutionary history leading to the current distribution, provides clear insights on diversification. The

taxonomic approach, based on the botanical expertise accumulated over centuries but neglecting relatedness, complements the phylogenetic approach, which is also imperfect, as the phylogenetic tree is based on partial knowledge and the complex evolutionary models for biome reconstruction are statistical estimations.

Growth forms and further trait research

Forest-savanna transitions were not consistently associated with a change in growth form, with clades mostly retaining their ancestral form. However, the

conservatism of growth form is undoubtedly overestimated, at least for clades that also include herbaceous species. Nevertheless, we identified some striking examples of labile clades whose presence in forest is associated with the diversification of climbing species (e.g. Combretaceae and *Strychnos*). Climbing habit is highly adapted to closed environments, allowing plants to reach the canopy and compete for light without growing large bodies (Schnitzer & Bongers, 2002). A precursor trait enabling this shift was recently revealed in the genus *Paullinia* (Sapindaceae) as a lobate primary bauplan promoting evolution towards variant secondary growths producing the compliant wood of lianas (Chery et al., 2020). Further research is needed to assess to what extent the African clades we highlighted share this precursor trait. We also identified labile genera and families whose presence in savanna is associated with the diversification of shrubby species, presumably because reducing height reduces hydraulic vulnerability (McDowell & Allen, 2015), a highly valuable adaptation to long and intense droughts in an environment where competition for light is low. Aside from changes in growth form, other mechanistic underpinnings that allowed lineages to diversify into novel environments need to be explored, such as the co-evolution of traits involved in xylem safety and desiccation delay strategies (Oliveira et al., 2019). Bark thickness, reproductive height and spinescence have also been linked to transition into the savanna biome, characterised by frequent fires and herbivory (Charles-Dominique et al., 2015). This work opens the door to further investigations of enabling traits for niche evolution, combining hard ecophysiological measurements, and soft traits, more easily measurable in field.

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AUTHORSHIP

A.-P.G., A.F., O.J.H., G.D. and K.S. designed the study. A.-P.G. performed the research. R.A.S. and K.G.D. developed the phylogeny of tropical tree genera, A.-P.G., K.G.D. and O.J.H. performed the phylogenetic analyses. All authors interpreted the results. A.-P.G. wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/ele.13985>.

DATA AVAILABILITY STATEMENT

The climatic niches of the 4154 species studied, as well as the list of bioclimatic groups to which they belong are openly available in DRYAD, reference number: <https://doi.org/10.5061/dryad.k98sf7m7f>.

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