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

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1 **Title:** Climatic niche lability but growth form conservatism in the African woody flora

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32 performed the phylogenetic analyses. All authors interpreted the results. A-P.G. wrote the first draft of  
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### 36 **Abstract**

37 Climatic niche evolution during the diversification of tropical plants has received little attention in  
38 Africa. To address this, we characterized the climatic niche of >4000 tropical African woody species,  
39 distinguishing two broad bioclimatic groups (forest vs. savanna) and six subgroups. We quantified niche  
40 conservatism *versus* lability at the genus level and for higher clades, using a molecular phylogeny of  
41 >800 genera. Although niche stasis at speciation is prevalent, numerous clades individually cover vast  
42 climatic spaces suggesting a general ease in transcending ecological limits, especially across bioclimatic  
43 subgroups. The forest biome was the main source of diversity, providing many lineages to savanna, but  
44 reverse shifts also occurred. We identified clades that diversified in savanna after shifts from forest.  
45 The forest-savanna transition was not consistently associated with a growth form change, though we  
46 found evolutionarily labile clades whose presence in forest or savanna is associated respectively with  
47 climbing or shrubby species diversification.

48

49

## 50 **Introduction**

51 Phylogenetic niche conservatism refers to a pattern whereby lineages retain ancestral ecological traits  
52 (Harvey & Pagel 1991). At a large scale, high levels of conservatism have been reported for plants (*e.g.*,  
53 in the southern hemisphere, Crisp *et al.* 2009; for the succulent biome, Ringelberg *et al.* 2020; and  
54 across the Americas, Segovia *et al.* 2020), demonstrating the prevalence of biome stasis at speciation,  
55 and designating niche conservatism as a key factor structuring the distribution of plant diversity. Even  
56 within the moist tropical forest biome, independent phylogenetic reconstructions of the niche of tree  
57 lineages were strongly correlated between continents, indicating a worldwide deep phylogenetic signal  
58 for the climatic niche (Hardy *et al.* 2012). However, many plant clades have transcended ecological  
59 barriers (Donoghue and Edwards 2014), as illustrated by the multiple evolutions toward C4  
60 photosynthesis in arid regions (over 45 times in 19 Angiosperm families, Sage 2004) and the recurrent  
61 adaptation of some ancestrally tropical clades to frost and temperate climates (Preston & Sandve 2013;  
62 Zanne *et al.* 2014). Large scale niche evolution is certainly easier for some clades and for some  
63 ecological transitions, but there is still a lack of general knowledge about these evolutionary patterns  
64 and processes.

65 Biomes are the most widely used vegetation units for studying large-scale niche lability as  
66 biome shifts are viewed as major transitions entailing significant adaptations (Donoghue & Edwards  
67 2014). The premise behind the biome concept is that the environment imposes, selects and filters for  
68 vegetation attributes, producing global vegetation units that are similar in physiognomy and function  
69 (Moncrieff *et al.* 2016). It has been proposed that robust biome definition requires the identification of  
70 traits with adaptive value and that are easily measurable on many species in many sites (Shipley *et al.*  
71 2016). However, trait-based biome delineation has been limited to a few traits, which may not entirely  
72 capture ecosystem structure and function (*e.g.* Conradi *et al.* 2020 using life forms in Africa). An  
73 alternative way is to group species that share similar environmental requirements, using ecological  
74 niche modelling (Broennimann *et al.* 2012), quantification of niche similarity (Warren *et al.* 2008) and  
75 statistically-driven clustering. Groups of species are predicted based on one simple overriding  
76 parameter, climatic niche similarity which encompasses the wide range of strategies that allow plants

77 to persist in particular conditions (Bilton et al. 2016). The divisions between such species groups  
78 (hereafter called “bioclimatic groups”) reflect significant ecological boundaries that have limited, and  
79 still limit, the distribution of some higher-level clades, but may be permeable to others through  
80 functional, and potentially clade-specific, adaptations.

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

89 On the African continent and elsewhere, despite the prevalence of niche conservatism in plants  
90 (Crisp *et al.* 2009; Linder *et al.* 2012; Segovia *et al.* 2020), many clades have transcended major  
91 ecological barriers, such as the forest-savanna boundary (see White 1978 for *Diospyros*; Gorel *et al.*  
92 2019 for *Erythrophleum* and references therein), but the direction, timing, functional trait association  
93 and distribution of such shifts over plant phylogeny have not been characterized at the scale of a whole  
94 flora. Here, we determined the climatic niche lability of the African tropical woody flora. We developed  
95 an approach to quantify niche conservatism *versus* lability, determining the climatic limits that constrain  
96 most clades and identifying which clades transcend these limits. Genus-level phylogenies were used to  
97 infer the timing and origin of the woody flora in the major bioclimatic groups (*i.e.* the forest and savanna  
98 biomes). We delineated bioclimatic groups based on species niche similarity by using published  
99 occurrence data in conjunction with climatic layers to model the climatic niche of >4000 woody species.  
100 We restricted our analysis to woody plants to grasp the common ecological and adaptive constraints of  
101 clades that share this life history strategy. We specifically ask the following questions.

102 How labile is climatic niche in the tropical woody flora? Numerous genera and families are  
103 expected to cover multiple bioclimatic groups at present and, from the Eocene, multiple shifts between

104 the forest and savanna biomes are expected above the genus level. We specifically expected an  
105 increasing proportion of forest to savanna biome shifts given the general trend of increasing aridification  
106 throughout the Cenozoic (Kissling *et al.* 2012).

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

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

## 116 117 **Material and methods**

### 118 Species occurrence and climatic layers

119 Occurrence data of native woody species were extracted from the RAINBIO database which contains  
120 593,861 georeferenced occurrences derived from herbarium vouchers collected across tropical Africa  
121 between 1782 and 2015, and representing 25,356 plant species (Dauby *et al.* 2016). The area covered  
122 from 20°N to 35°S is broadly defined as sub-Saharan Africa excluding South-Africa and Madagascar.  
123 Most of the species (91%) have been scored for growth form (tree, shrub, shrublet, herb, climber, liana,  
124 vine, epiphyte and parasitic). Occurrences of exotic/cultivated species or specimens collected in  
125 botanical gardens or equivalent were removed as well as occurrences without identification down to the  
126 species level and with poor georeferencing accuracy (“accuracy”  $\leq 3$ ). Since we were interested in  
127 woody species, we considered genera containing species scored as “tree”, “shrub”, “shrublet”, “vine”,  
128 “climber” and “liana”. For genera with only species assigned to “climber” and “vine” forms, flora and  
129 herbarium specimen were consulted to determine woodiness. The **woody** species lists from Fayolle *et*  
130 *al.* (2014, 2019) for forest and savanna sites, respectively, were also included, resulting in a combined

131 dataset containing the occurrences of 8,232 species belonging to 1,292 genera and 169 families (329,381  
132 occurrences). The taxonomy followed the original RAINBIO database (Dauby *et al.* 2016) with the  
133 exception of the African Acacias that were assigned to either *Vachellia* or *Senegalia* following  
134 Kyalangalilwa *et al.* (2013).

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

140

141 Niche modeling

142 To select the most appropriate climatic space to model species niches, we first performed a Principal  
143 Component Analysis (PCA) using the pixel values of the climatic layers for the whole African  
144 continent. In the space defined by the first two axes, we projected the scores of the pixels with at least  
145 one species occurrence and estimated kernel densities. For subsequent niche modelling, the climatic  
146 background corresponds to the values of the principal components within the 99% kernel densities, to  
147 avoid bias due to species occupying extreme environments while keeping the maximum number of  
148 species. In addition, we kept only species with at least 90% of occupied pixels inside the selected  
149 climatic background to avoid bias due to incomplete coverage of their distribution (7,928 species, 1,260  
150 genera, 167 families).

151 The niche of each species was then delineated within the climatic space defined by the first two  
152 axes of the PCA calibrated with the selected climatic background (Broennimann *et al.* 2012). The two  
153 principal components correspond to two main environmental gradients (Fig. S1). A mean temperature  
154 gradient (44.4% variance explained) opposed warmer areas with higher potential evapotranspiration  
155 (positive scores) to cooler areas (negative scores) and a rainfall/temperature seasonality gradient (34.6%  
156 variance explained) opposed drier areas with high temperature seasonality (positive scores) to wetter  
157 and more isothermal areas (negative scores). PCA scores were obtained for all occurrences and at this

158 stage, we retained the species with at least seven climatically unique occurrences (4,155 species; 960  
159 genera; 138 families, totaling 288,412 occurrences). For each species, the PCA scores of the  
160 occurrences were projected onto a grid of cells bounded by the minimum and maximum scores in the  
161 climatic space. The species niche was defined as the smoothed density of occurrences in each cell of  
162 the grid estimated using a kernel density function.

163

#### 164 Species clustering

165 To group species according to their climatic niche, we first created a niche dissimilarity matrix. To  
166 quantify niche overlap among all pairs of species, we used the Hellinger's I statistic (Warren *et al.*  
167 2008). The overlap varies between 0 (no overlap) and 1 (complete overlap, identical niches). The  
168 corresponding dissimilarity matrix (1-I) was built containing the value of niche dissimilarity for all pairs  
169 of species retained (4,155 species  $\times$  4,155 species). A non-metric multidimensional scaling (NMDS,  
170 results not shown) was used to visualize the niche dissimilarity into a two-dimensional space and at this  
171 stage, we excluded from the dataset 13 species whose distributions were centered in the Kalahari desert  
172 (at the edge of the RAINBIO geographical coverage). A hierarchical clustering approach was used for  
173 grouping the 4,142 retained species (956 genera, and 138 families) occupying similar climates, whether  
174 or not they are found in the same geographical area. We used Ward's algorithm for creating the  
175 dendrogram representing niche (dis-)similarity among species. A silhouette analysis was used to choose  
176 the optimal number of clusters (Fig. S2) and we retained two and six bioclimatic groups and subgroups,  
177 respectively, that were mapped in the climatic and geographic spaces by calculating for each pixel the  
178 proportion of species assigned to one bioclimatic (sub)group. Only species with a positive silhouette  
179 width, *i.e.*, well assigned to the (sub)group, not transitional, were used (n=3,997 species for the two  
180 groups, n=3,476 for the six subgroups). A resolution of 75 arc minute was used for the geographical  
181 space.

182

#### 183 Ancestral biome reconstruction



184 We developed a genus-level phylogeny following Segovia *et al.* (2020) and Sanchez-Martinez *et al.*  
185 (2020) in which the species were attached to their respective genus as polytomies (Fig. S10). We did  
186 not consider large-scale phylogenies resolved to the species level because they are still largely based on  
187 plastid markers and their topologies are not reliable for many genera due to recurrent chloroplast  
188 captures (see references in SI). The final dataset consisted of 813 genera (85% of coverage) and 3,639  
189 species mapped onto the time-calibrated phylogeny. Ancestral biomes (*i.e.* the major bioclimatic  
190 groups, forest vs savanna) were reconstructed with generalized Markov models, without and with  
191 hidden states (Boyko & Beaulieu 2021). The complete model selection procedure is given in SI as well  
192 as the phylogeny with marginal reconstructions (Fig. S10). We focused on a single rate (ER) model  
193 across the phylogeny. At each node, the most likely biome state was estimated. The ER model  
194 predictions have been compared with those of the AIC-supported ARD/ARD model (Table S5, S6 and  
195 Fig. S9).

#### 196 Data analyses

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

206 To examine how niche lability varies across ecological boundaries, the ease of transition  
207 between all pairs of bioclimatic (sub)groups was inferred by their current taxonomic similarity. We  
208 computed the Simpson similarity index at genus and family levels (the number of shared genera/families  
209 divided by the number of genera/families occurring in the smaller sample). The link between the  
210 taxonomic similarity of bioclimatic (sub)groups and their environmental and geographical distances

211 (estimated as the Hellinger's I overlap of cluster projections) was tested using Spearman correlation  
212 tests.

213 To examine how niche lability varies across clades, we first identified the most ecologically  
214 diverse genera and families at present and evaluated how species richness in genera and families varied  
215 with niche lability. To avoid sampling bias, we used sample-based rarefaction to estimate the number  
216 of subgroups occupied by each genus and family when resampling six species, and tested whether it  
217 increased with total species richness (using Spearman correlation test), as expected if past niche shifts  
218 tend to increase the diversification rate. We also tested the effect of clade ages. Then, we further  
219 investigated shifts between the forest and savanna biomes by identifying clades which currently have  
220 more forest (or savanna) species than expected by chance using an exact test of goodness of fit with an  
221 assumed probability of 0.70 for forest and 0.30 for savanna (*i.e.*, matching the proportion of forest and  
222 savanna species in the dataset). Based on the ancestral biome reconstruction since 50Ma, we estimated  
223 the proportion and timing of shifts for each order and family (with more than three genera).

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

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

238

## 239 **Results**

### 240 Climatic niches

241 The species were divided into two major bioclimatic groups (Fig. 1) differentiated along the  
242 rainfall/temperature seasonality gradient. **These two bioclimatic groups closely match the forest and the**  
243 **savanna biomes as shown by earlier maps (Fig. S5a,b) and by the proportion of species assigned to each**  
244 **bioclimatic group in locations where *in-situ* habitat is known (Fig. S5d).** The first major bioclimatic  
245 group, *i.e.* the forest biome, was divided into three subgroups while the second major bioclimatic group,  
246 *i.e.* the savanna biome, was composed of two large savanna subgroups. A third smaller subgroup found  
247 along the Indian Ocean coastal belt (Fig. 1a), hereafter referred as the “Coastal” subgroup, was treated  
248 separately because it is a mosaic of forest and savanna. See in SI the distribution of the bioclimatic  
249 groups in climatic and geographic space (Fig. S3, S4), as well as the contributions of the climatic  
250 variables to the bioclimatic groups’ delimitation (Table S1).

251 The forest biome occupied the wettest and more isothermal areas (Fig. 1a) and its distribution  
252 extended from West to Central Africa (Fig. 1c). This hyperdiverse biome included 2,630 species from  
253 673 genera and 104 families. Of these, 207 genera and 18 families were polytypic and conserved (*i.e.*,  
254 with all their species in the forest biome). The most diverse among the conserved genera and families  
255 were respectively *Gilbertiodendron* (Fabaceae, 20 species) and Lecythidaceae (24 species). The “Wet  
256 Forest” subgroup was typical of the climatic conditions encountered in Gabon (Fig. 1c). The “Moist  
257 Forest”, the most diverse and conserved of the “Forest” subgroups (Fig. 1d, e), occupied a wider  
258 climatic and geographical area, both in West and Central Africa (Fig. 1a, c). Finally, the species of the  
259 “Dry Forest” subgroup were associated with the drier and warmer conditions of West Africa, over an  
260 area that largely overlapped the area occupied by the “Moist Forest” but extended further north (Fig.  
261 1c).

262 The savanna biome occupied the driest areas and a wide range of temperatures, from the coldest  
263 to the hottest regions (Fig. 1a). Species were found in both Eastern, Western and Southern Africa (Fig.  
264 1c). This biome was less diverse in terms of woody species than the “Forest” group, comprising 1,135

265 species in 443 genera and 107 families. Of these, 69 genera and 14 families were polytypic and  
266 conserved, the most diversified being *Commiphora* (Burseraceae, 22 species) and Proteaceae (7  
267 species). The “Cold Savanna”, the most diverse and conserved of the “Savanna” subgroups (Fig. 1d, e),  
268 had a very wide climatic breadth, composed of species present in the coldest and in the most arid  
269 conditions in Eastern and Southern Africa. The “Hot Savanna” subgroup occupied the warmest and  
270 driest conditions in West Africa (Fig. 1a, c).

271 The “Coastal” subgroup was found in the Indian Ocean coastal belt. Although associated with  
272 a savanna-prone climate, the vegetation actually is a forest-savanna mosaic partly driven by complex  
273 topography (Burgess *et al.* 1998), which is not captured in our analysis due to the coarse resolution we  
274 used. This group **showed little evidence for conservatism** (Fig. 1d, e), with no conserved families and  
275 very few genera, the most diverse being *Hilsenbergia* (Boraginaceae, three species).

276

#### 277 Niche lability across time

278 Considering that 84% of the polytypic genera (n=436) and 84% of the polytypic families (n=94) had  
279 species in at least two bioclimatic subgroups, niche lability can be considered common. Likewise, 43%  
280 of the polytypic genera (n=210) and 70% of the polytypic families (n=76) had species in both the forest  
281 and savanna biomes. Since 50Ma at supra-genus level, **the ER model predicted** biome shifts for 7% of  
282 the 917 speciation events, the majority being from forest to savanna (74% of shifts, Fig. 2, Table S2).  
283 The forest biome was conserved in 75% of the events and the savanna biome in 18%. While the number  
284 of speciation events increase since 50Ma, the proportion of shifts remains relatively constant (Fig. 2c).  
285 Forest was the most likely ancestral biome of the majority of genera occurring both in forest and savanna  
286 (73%). **Similar results were obtained with an ARD/ARD model (Table S5-S6, Fig. S9).**

287

#### 288 Niche lability across bioclimatic groups

289 The ease of transition between all pairs of bioclimatic (sub)groups was inferred by their current  
290 taxonomic similarity. Between the forest and the savanna biomes, the taxonomic similarity (measured  
291 with the Simpson index) was 0.47 for genera and 0.73 for families. Between subgroups, similarity

292 ranged from 0.22 to 0.65 for genera (Fig. 1d) and similarity increased with environmental proximity  
293 ( $r_s=0.79$ ) and, to a lesser extent, with current geographic proximity ( $r_s=0.65$ ). These relationships were  
294 weaker for families ( $r_s=0.44$  and  $0.46$  for environmental and geographic overlap, respectively)  
295 indicating that most families were found in the subgroups, regardless of the current geographical and  
296 environmental proximity (Fig. 1e). The highest similarity was found between the “Cold Savanna” and  
297 the “Hot Savanna” subgroups. The “Coastal” subgroup had an intermediate composition between forest  
298 and savanna, sharing many genera and families both with the “Moist Forest” and with the “Cold  
299 savanna” (Fig. 1d, e).

300

### 301 Niche lability across clades

302 Across clades, niche lability increased with species richness, with more species-rich genera (families)  
303 being more ecologically diverse (Fig. 3). When controlling for sample size by subsampling six species  
304 per genus (and family), the expected number of occupied bioclimatic subgroups was positively  
305 correlated with total species richness (Fig. S6), but no significant correlation was detected with genus  
306 (-family) age. Twelve genera and 23 families were found to be so ecologically labile that they have  
307 species across all six bioclimatic subgroups. This is particularly true for the hyperdiverse *Combretum*  
308 ( $n=86$  species), *Ficus* ( $n=59$ ) and *Cola* ( $n=45$ ) genera (Fig. 3a), and for the hyperdiverse Rubiaceae and  
309 Fabaceae families (Fig. 3b).

310 Current patterns of biome conservatism and specialization (Fig. 4) were related to contrasting  
311 evolutionary histories and lability across clades (Fig. 2, Table S2). The majority of clades currently  
312 have more species in the forest than in the savanna biome (Fig 4), as the result of very high forest  
313 conservatism since 50Ma (Fig. 2a, b). The Magnoliales (including the Annonaceae family), with a large  
314 majority of speciation events within the forest biome (97%), was one of the most forest conserved but  
315 hyper-diversified orders (Fig. 2). The proportion of species in forest versus savanna for most clades did  
316 not differ significantly from that expected by chance (90% of genera, 70% of families, 60% of orders,  
317  $P \leq 0.05$ ), although we found several savanna-specialized families and orders (Figs. 2b, 4). Some of  
318 them, such as the Lamiales, displayed high levels of savanna conservatism at speciation events (80%)

319 but also reverse shifts from savanna to forest (17%). Others, such as the Fabales (and Fabaceae), while  
320 having high forest conservatism (80% of the speciation events), have shifted many times from forest  
321 to savanna (10%), which explains the current presence of many savanna-specialized lineages (Fig. 2b).  
322 The Malpighiales, currently forest-specialized (Fig. 2b), was also characterized by forest conservatism  
323 (80% speciation events), but showed lower levels of shifts, mostly from forest to savanna (5%).

324

#### 325 Growth form lability

326 The forest and the savanna biomes were both half composed of tree species. Proportionally, the forest  
327 biome was richer in climbers than the savanna biome (26% vs. 8%, respectively), and the savanna biome  
328 was richer in shrubs (40% vs. 23%, respectively). Only half of the labile genera presented multiple  
329 growth forms, and rarely all three forms (10%, Fig. 5). For labile families, change in growth form was  
330 more frequent (84%). Using the complete dataset and binomial mixed models, we did not detect  
331 significant ecological convergence in growth forms, but instead evidence for high conservatism at the  
332 genus level and, to a lesser extent, at the family level (Table 1). Conservatism at genus level was  
333 particularly strong for the climber growth form. Considering each labile genus and family separately,  
334 forest-savanna transitions were significantly associated with changes in the distribution of growth forms  
335 for seven genera and 12 families (Fisher's test  $P < 0.05$ , names given in Fig. 5), with significantly more  
336 climbers in the forest biome (n=5 genera, n=8 families) and more shrubs in the savanna biome (n=5  
337 genera, n=9 families).

338

## 339 Discussion

340

### 341 Climatic niches across the African tropical woody flora

342 In this study, we clustered 4,142 woody species of tropical Africa according to their climatic niche  
343 similarity and the first division we obtained corresponds to the forest and savanna biomes. This result  
344 demonstrates that grouping species that share similar environmental requirements is a good alternative  
345 to using traits to approximate a common response to environment, though we recognize that forests and  
346 savannas can co-exist under a wide range of climates (Staver *et al.* 2011), where they can be alternative

347 stable states maintained by feedbacks between tree cover and fire. Our method has a clear advantage in  
348 delineating meaningful groups within biomes, especially for forests, where differences in structure and  
349 function are subtle and not always easy to detect by remote sensing. We also identified six different  
350 subgroups which represent the main climatic boundaries within biomes. The subgroups are distributed  
351 respectively along a precipitation/temperature seasonality gradient and a mean temperature gradient,  
352 two gradients strongly associated with variation in woody species composition (Fayolle *et al.* 2014,  
353 2019). The “Dry Forest” subgroup supports the existence of a flora adapted to seasonal drought stress  
354 in West Africa (Swaine 1992). Within savanna, the “Hot” and the “Cold savanna” subgroups  
355 corresponds to the floristic turnover associated with the steep change in altitude and temperature  
356 (Fayolle *et al.* 2019). The “Cold savanna” encompasses floristic heterogeneity (Linder *et al.* 2012)  
357 which is certainly not purely determined by climate but related to other environmental factors (*e.g.* soils,  
358 fire and herbivory).

359

360 Niche lability

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

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

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

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

398 The extent of niche lability is uneven across clades, and we have shown that the richest genera  
399 (and families) are generally the most ecologically diverse (apart from *Searsia*), a pattern robust even  
400 after taking into account sampling bias. As the age of the clades does not explain these differences, this



401 result could be evidence of contrasting abilities to evolve and diversify in multiple environments. The  
402 ancestral character of the forest biome combined with a high level of conservatism explains the current  
403 higher species richness in the forest biome for a majority of clades, as has been reported before  
404 (Eiserhardt *et al.* 2017). Nevertheless, we highlighted some clades, such as the Fabaceae, that have been  
405 particularly successful at diversifying in drier conditions after multiple shifts from forest and **currently**  
406 hold multiple savanna-specialist lineages. We also identify clades (*e.g.* Lamiales, Asterales) which are  
407 highly specialized to forest or savanna, with a particularly high biome stasis during speciation since the  
408 Eocene. For savanna-specialized clades, diversification into African savannas may have been preceded  
409 by intercontinental migrations with niche conservatism (Panero & Crozier 2016 for the Asteraceae).  
410 **The best way to explore the diversification of the flora would come from well-resolved species-level**  
411 **phylogenies, but we simply do not have enough of them for the African flora. However, we show that**  
412 **combining a taxonomic approach, *i.e.* dissecting the current distribution of clades, with genus-level**  
413 **phylogenetic approach to infer the evolutionary history leading to the current distribution, provides**  
414 **clear insights on diversification. The taxonomic approach, based on the botanical expertise accumulated**  
415 **over centuries but neglecting relatedness, complements the phylogenetic approach, which is also**  
416 **imperfect, as the phylogenetic tree is based on partial knowledge and the complex evolutionary models**  
417 **for biome reconstruction are statistical estimations.**

418

419 Growth forms and further trait research

420 Forest-savanna transitions were not consistently associated with a change in growth form, with clades  
421 mostly retaining their ancestral form. However, the conservatism of growth form is undoubtedly  
422 overestimated, at least for clades that also include herbaceous species. Nevertheless, we identified some  
423 striking examples of labile clades whose presence in forest is associated with the diversification of  
424 climbing species (*e.g.*, Combretaceae and *Strychnos*). Climbing habit is highly adapted to closed  
425 environments, allowing plants to reach the canopy and compete for light without growing large bodies  
426 (Schnitzer & Bongers 2002). A precursor trait enabling this shift was recently revealed in the genus  
427 *Paullinia* (Sapindaceae) as a lobate primary bauplan promoting evolution towards variant secondary

428 growths producing the compliant wood of lianas (Chery *et al.* 2020). Further research is needed to  
429 assess to what extent the African clades we highlighted share this precursor trait. We also identified  
430 labile genera and families whose presence in savanna is associated with the diversification of shrubby  
431 species, presumably because reducing height reduces hydraulic vulnerability (McDowell & Allen  
432 2015), a highly valuable adaptation to long and intense droughts **in an environment where competition**  
433 **for light is low**. Aside from changes in growth form, other mechanistic underpinnings that allowed  
434 lineages to diversify into novel environments need to be explored, such as the co-evolution of traits  
435 involved in xylem safety and desiccation delay strategies (Oliveira *et al.* 2019). Bark thickness,  
436 reproductive height and spinescence have also been linked to transition into the savanna biome,  
437 characterized by frequent fires and herbivory (Charles-Dominique *et al.* 2015). **This work** opens the  
438 door to further investigations of enabling traits for niche evolution, combining hard ecophysiological  
439 measurements, and soft traits, more easily measurable in field.

440

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- 582

583 **Tables**

584 Table 1 Variance explained by fixed and random effects for models testing the relative effects of  
 585 evolutionary convergence (“Savanna” group versus “Forest” group, as fixed effect) and phylogenetic  
 586 conservatism (family and genus as random effects) on growth forms: tree, shrub and climber

Models	Fixed variance (%)	Random variance (%)	Residual variance (%)
tree~ biome+ (1 fam)	0.01	52.30	47.69
tree~ group + (1 genus)	0.06	71.52	28.42
shrub~ group + (1 fam)	3.01	21.25	75.74
shrub~ group + (1 genus)	3.09	53.52	43.39
climber~ group + (1 fam)	2.80	63.23	33.97
climber~ group + (1 genus)	0.58	97.80	1.62

587

## 588 **Figures**

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

607

608 Figure 2 Biome lability across time. (a) Ancestral biome reconstruction for woody Angiosperms. The  
609 tree was colored according to the most likely states of nodes (green: forest, orange: savanna) and some  
610 ancestral nodes corresponding to taxonomic orders were highlighted. The complete phylogenetic tree  
611 for Angiosperms and the few Gymnosperms we studied is given in SI (Fig. S10). (b) The current biome  
612 specialization (more species in one biome than expected by chance) and conservation are given for  
613 genus, family and orders with the same color coding as Fig. 4: orange and pale green clades have more  
614 species, respectively in Savanna and Forest, than expected by chance (hereafter called savanna- and

615 forest-specialized clades). Red and dark green clades are totally conserved, respectively in savanna and  
616 forest. Blue clades have a forest-savanna species distribution that do not differ significantly from that  
617 expected by chance. (c) Timing of speciation events and shifts since 50 Ma for all lineages and four  
618 highly diversified orders. The bars represent the number of speciation events on our phylogeny (left  
619 axis) and the line represents the percentage of speciation events associated with biome shifts (right axis).  
620

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

626  
627 Figure 4 Species richness in the “Savanna” group compared to species richness in the “Forest” group  
628 for genera (dots, names in lower case and italics), families (triangle, names in lower case) and orders  
629 (diamond, names in upper case). The size of the symbols is proportional to the number of genera,  
630 families or orders and the names of the most diverse genera, families and orders are shown. The solid  
631 line represents the null 70:30 ratio: the number of forest vs savanna species as expected by chance, *i.e.*,  
632 following the proportion of species in forest and savanna in the whole dataset. The blue shaded area  
633 corresponds to values that do not differ significantly from that expected by chance. Orange and pale  
634 green clades have more species, respectively in Savanna and Forest, than expected by chance (*i.e.*  
635 savanna- and forest-specialized clades). Red and dark green clades are totally conserved, respectively  
636 in savanna and forest. The dotted lines represent the 1:1 ratio.

637  
638 Figure 5 For each labile genus (dots, name in italic) and family (triangles), the percentage of trees,  
639 shrubs and climbers in the “Forest” group (green symbols) and in the “Savanna” group (red symbols).  
640 The size of the symbols reflects the number of genera or families with the same values. The lines  
641 connect the two symbols for each genus or family and indicate the Forest-Savanna shifts in growth



642 forms (longer lines indicate larger shifts in growth form). The names of the genera and families having  
643 a significant change in the distribution of growth forms across the two biomes (according to the Fisher  
644 test,  $P \leq 0.05$ ) are given with the line colored black.