

Ecological niche divergence associated with species and populations differentiation in *Erythrophleum* (Fabaceae, Caesalpinioideae)

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Background and aims – The isolation of populations inside forest refugia during past climate changes has widely been hypothesized as a major driver of tropical plant diversity. Environmental conditions can also influence patterns of diversity by driving divergent selection leading to local adaptation and, potentially, ecological speciation. Genetic and phylogenetic approaches are frequently used to study the diversification of African tree clades. However, the environmental space occupied by closely related species or intra-specific gene pools is barely quantified, though needed to properly test hypotheses on diversification processes.

Methods – Using species distribution models, we determined the bioclimatic constraints on the distribution of closely related species and intra-specific gene pools. Our study model, *Erythrophleum* (Fabaceae – Caesalpinioideae), is a tropical tree genus widespread across Africa, and vastly investigated for genetics. Here, we combined the available phylogenetic data with information on niche divergence to explore the role of ecology into diversification at the species and gene pool levels.

Key results – Ecological speciation through climate has probably played a key role in the evolution of the *Erythrophleum* species. The differential climatic niche of the species indicated adaptive divergence along rainfall gradients, that have probably been boosted by past climate fluctuations. At the gene pool level, past climate changes during the Pleistocene have shaped genetic diversity, though within *Erythrophleum suaveolens*, adaptive divergence also occurred.

Conclusions – We believe that ecological speciation is a key mechanism of diversification for tropical African tree species, since such climatic niche partition exist among many other genera. Modelling the environmental niche of closely related taxa, and testing for niche differentiation, combined with divergence dates offered new insights on the process of diversification.

Key words – Ecological divergence, ecological speciation, *Erythrophleum*, forest refuge hypothesis, gene pools, local adaptation, MaxEnt Algorithm, niche divergence, rainfall gradients, African tropical trees.

INTRODUCTION

In the tropics, and specifically in Africa, the spatial patterns of species diversity (Lönnerberg 1929, Mayr & O'Hara 1986, Sosef 1994, Linder 2014) and of intra-specific genetic diversity (Hardy et al. 2013, Duminil et al. 2013) have frequently been interpreted in the light of past climate changes. The forest refuge hypothesis postulates that climate-driven expansions and contractions of lowland forests during glacial periods, especially during the last glacial episode of the Pleistocene (i.e. 120000 to 12000 years BP), led to diversification (Mayr & O'Hara 1986, Sosef 1994, Hardy et al. 2013). The contraction of forests inside refugia during the glacial maxima would have driven allopatric speciation or, at least, genetic differentiation between fragmented populations (Maley 1996). Hosting a high number of endemic species, areas such as hilly and mountainous regions, have been proposed as candidate forest refugia (e. g. Sosef 1994).

Environmental conditions can affect the inter- and intra-specific diversity by driving divergent selection on traits (Nosil 2012). Natural selection may contribute to ecological divergence both in presence or absence of geographic isolation between populations (Graham et al. 2004, Simões et al. 2016). At regional scale, ecological divergence between related species have already been supported for animals (Losos et al. 2003, Graham et al. 2004, Knouft et al. 2006, Blair et al. 2013) and for plants (Schnitzler et al. 2012, Dauby et al. 2014). In tropical Africa, there is a strong support of the role of climatic gradients as drivers of diversity. Rainfall represents the most important environmental gradient at both regional and continental scales and has been demonstrated to determine species distribution (Swaine 1996, Bongers et al. 1999) and floristic composition in forests (Fayolle et al. 2014) and savannas (Fayolle et al. 2019).

Genetic and phylogenetic approaches are frequently used to study the diversification of African tree clades (Hardy et al. 2013), but the environmental space occupied by congeneric species or intra-specific gene pools is, however, barely quantified (but see Couvreur et al. 2011 for *Isolona* and *Monodora*, Holstein & Renner 2011 for *Coccinia*). Quantifying the ecological divergence between related species or gene pools is fundamental to properly support the role of ecology into diversification (Graham et al. 2004). At species level, ecological divergence is one of the baseline evidence needed to support a case of ecological speciation (Rundell & Price 2009, Nosil 2012). At gene pool level, ecological divergence provides an ecological basis for the assertion that environmental variation may be driving local adaptation.

In this study, we investigated the diversification processes between species and gene pools within *Erythrophleum* (Fabaceae, Caesalpinioideae). *Erythrophleum* is a pantropical tree genus represented by four parapatric species in tropical Africa: *Erythrophleum ivorense* A.Chev, *E. suaveolens* (Guill. & Perr.) Brenan, *E. africanum* Harms (Gorel et al. 2015, fig. 1A) and *E. lasianthum* Corbishley (not studied here, restricted range in South-East Africa). *Erythrophleum ivorense* is restricted to wet evergreen forest in the southern parts of the Upper and Lower Guinean Subcentres of the Guineo-Congolian Centre (White 1978, 1983) with a disjunct distribution, being absent from the arid Dahomey Gap,

a coastal savanna corridor about 100 km wide separating the two Subcentres. *Erythrophleum suaveolens* is widespread across tropical Africa, being distributed from the entire Guineo-Congolian Centre to the Zambezi Centre, with the notable exception of the wet forest areas that are occupied by *E. ivorense* (Duminil et al. 2010). *Erythrophleum africanum* is broadly present in the Sudanian and Zambezi Centres and Transition Zones around the Guineo-Congolian Centre. In the Upper and Lower Guinean Subcentres, a strong spatial genetic structure, mainly parapatric, has been demonstrated within both *E. ivorense* and *E. suaveolens* (Duminil et al. 2013, fig. 1B). Analyses of demographic reconstruction and molecular dating suggest that the divergence between gene pools was contemporaneous of the Pleistocene climatic cycles (Duminil et al. 2015), congruent with the forest refuge hypothesis. However, the possible role of adaptive divergence at the inter-specific level or as a complementary mechanism at the intra-specific level still needs to be investigated.

Using species distribution models (SDMs) we determined the bioclimatic constraints on the distribution of the *Erythrophleum* species across tropical Africa, and of *E. ivorense* and *E. suaveolens* gene pools in the Upper and Lower Guinean Subcentres. We combined the available phylogenetic data with information on ecological niche divergence to explore the role of ecology into diversification. We specifically tested whether the adaptation to specific climatic conditions played a role in the distribution and diversification. The adaptation in response to climate is expected to result in species/pools pairs adapted to different habitat and presenting clear climatic niche divergence (Graham et al. 2004).

METHODS

Occurrence data

We used two sets of occurrence data at the species and at the gene pool levels. At the species level, a total of 606 georeferenced occurrence data (*E. ivorense*, n = 150, *E. suaveolens*, n = 206 and *E. africanum*, n = 250, fig. 1A) were available from herbarium databases [Conservatoire et Jardin botaniques de la Ville de Genève (CJB) and the South African National Biodiversity Institute (SANBI)]. These samples cover the whole range of each species. At the gene pool level, 148 georeferenced occurrence data were provided from a genetic dataset (Duminil et al. 2013) for the two rainforest species, *E. suaveolens* and *E. ivorense* in the Upper and Lower Guinean Subcentres. The genetic samples covered only a restricted part of the species range. Duminil et al. (2013) identified three gene pools for *E. ivorense* and three gene pools for *E. suaveolens*. Within each species, the gene pools were distributed in West Africa (*E. ivo W* and *E. sua W* respectively for *E. ivorense* and *E. suaveolens*), in the northern part of central Africa (*E. ivo Cn* and *E. sua Cn*, respectively) and in the southern part of central Africa (*E. ivo Cs* and *E. sua Cs*, respectively, fig. 1B). Before modelling, we trimmed the occurrences data so that only one point was kept per grid cell of 1 km². After trimming, the low number of unique occurrence available for *E. ivo W* (n < 5) prevented the modelling of its potential distribution.

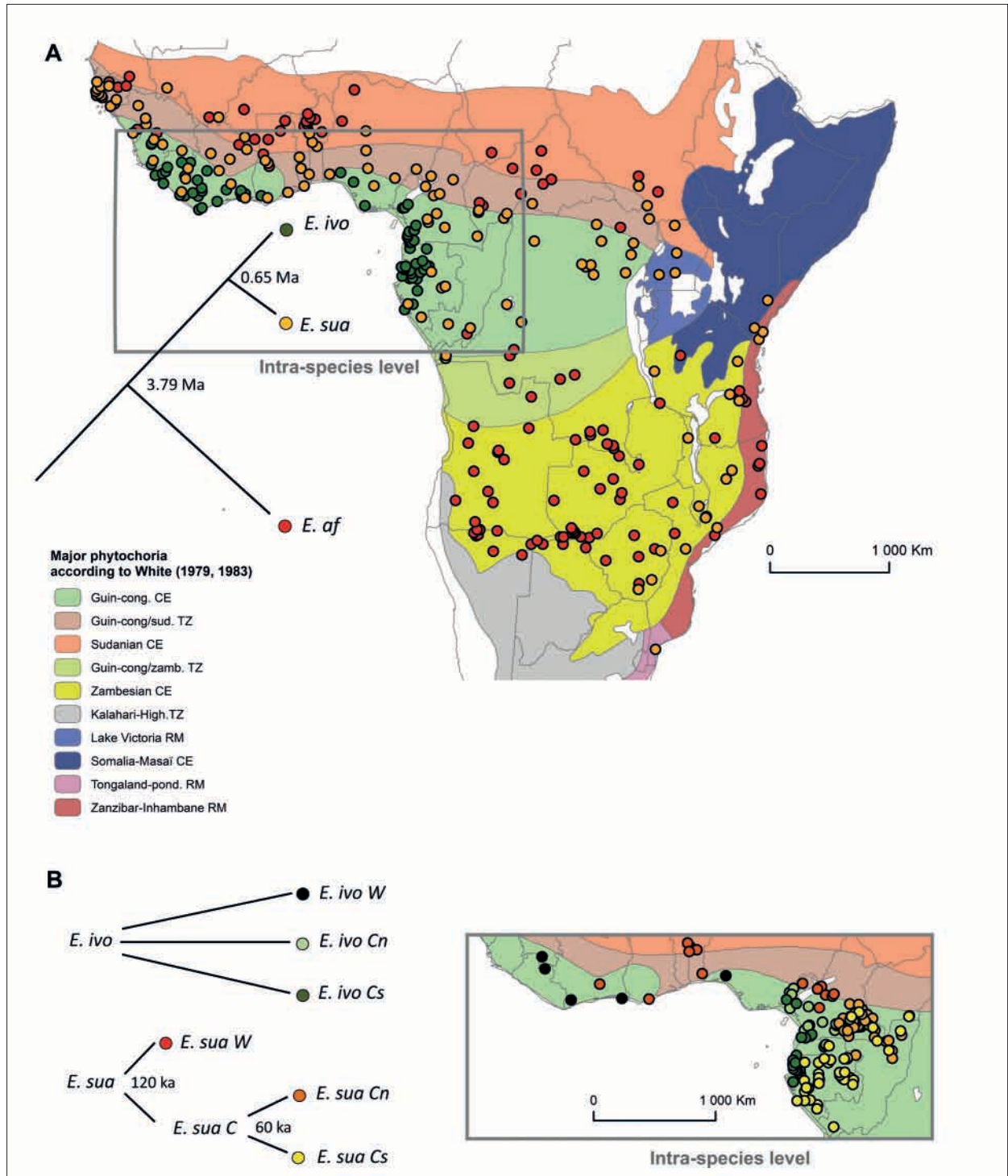


Figure 1 – Schematic cladograms and distribution of tropical African *Erythrophleum* species (A) and gene pools (B). The SDMs of the species *E. ivorensis* (*E. ivo*, $n = 150$), *E. suaveolens* (*E. sua*, $n = 206$), *E. africanum* (*E. af*, $n = 250$) were built for sub-Saharan Africa with occurrence data provided by herbarium samples. The SDMs of the gene pools were built for the Upper Guinean Subcentre (West Africa) and the Lower Guinean Subcentre (Atlantic Central Africa) with occurrence data from a genetic dataset (Duminil et al. 2013) and provided by the authors. Occurrence of gene pools were available for West Africa *E. ivorensis* (*E. ivo W*, $n = 23$), northern Central Africa *E. ivorensis* (*E. ivo Cn*, $n = 60$), southern Central Africa *E. ivorensis* (*E. ivo Cs*, $n = 48$), West Africa *E. suaveolens* (*E. sua W*, $n = 40$), northern Central Africa *E. suaveolens* (*E. sua Cn*, $n = 247$) and southern Central Africa *E. suaveolens* (*E. sua Cs*, $n = 87$). Occurrence data overlaid on a base map showing the boundaries of the major phytochoria according to White (1983; Mollweide projection) with abbreviations corresponding to Centre of Endemism (CE), Regional Mosaic (RM) and Transition Zone (TZ). Dates of divergence according to Duminil et al. (2015) are indicated on the cladograms.

Environmental data

To characterize the environmental space used by the species and gene pools, we gathered the 19 Bioclim variables and one altitudinal layer at the resolution of 10 arc minute for distribution models at the species level across the whole tropical Africa and of 2.5 arc minute for distribution models at the gene pool level across the Upper and Lower Guinean Sub-centres (Hijmans et al. 2005). To reduce collinearity between environmental variables and the risk of overfitting, we used a subset of nine weakly correlated variables ($r_{\text{Pearson}} < 0.70$, the Pearson correlation table is given in electronic appendix 1). The nine variables retained were altitude (alt, in m), annual mean temperature (Bio1, in $^{\circ}\text{C} \times 10$), isothermality (Bio3, unit-less), temperature annual range (Bio7, in $^{\circ}\text{C} \times 10$), annual precipitation (Bio12, in mm), precipitation seasonality (Bio15, in mm), precipitation of driest quarter (Bio17, in mm), precipitation of warmest quarter (Bio18, in mm) and precipitation of coldest quarter (Bio19, in mm).

Species distribution modelling

To model the environmental niche of the species and gene pools, we used the MaxEnt algorithm (Phillips et al. 2006) within the R environment (R version 3.2.3, R Core Team, Vienna, Austria). To reduce the influence of bias in the spatial sampling of occurrence data we used the weighted-target group approach (Anderson 2003). The weighted-target group approach consists in selecting background data from points that reflect a sample selection bias similar to that of the occurrence data. We used as background, occurrence data from herbarium and genetic samples of species others than *Erythrophleum*. Data from herbarium samples were downloaded from the GBIF database (<http://www.gbif.fr>) and included all the records available for Angiosperms in Africa. Data from genetic samples (Hardy et al. 2013) were kindly provided by the “Plant population genetics and community diversity in tropical rainforests” group (Université Libre de Bruxelles, Belgium).

We conducted species- and gene pool-specific tuning for the three species and for the five gene pools studied using the R package ‘ENMeval’ (Muscarella et al. 2014). We built SDMs with regularization multipliers ranging from 0.5 to 3 (increment 0.5) and from 4 to 6 (increment 1) and with six different feature-class combinations (L, LQ, H, LQH, LQHP, LQHPT; where L corresponds to linear, Q to quadratic, H to hinge, P to product and T to threshold). The Akaike Information Criterion (AIC) was used for model selection. The performance of the selected models was evaluated using four criteria, the Minimum Training Presence omission rate (OR_{mtp}), the True Skill Statistic (TSS, Allouche et al. 2006), the AUC_{test} and the AUC_{diff} . The AUC_{test} corresponds to the threshold-independent metric Area Under the receiver operating characteristic Curve (Hanley & McNeil 1982). The AUC_{diff} corresponds to the difference between AUC values based on training localities and AUC_{test} (Warren & Seifert 2011). These criteria were obtained using the ‘checkerboard2’ approach of data partitioning (Muscarella et al. 2014).

Quantifying niche overlap and conservatism

We quantified and tested the niche conservatism or divergence among pairs of related species and gene pools. Pairs have been constructed by minimizing the phylogenetic and the geographic distances. Niche overlap among pairs was estimated using the Schoener’s D statistic (Schoener 1968, Warren et al. 2008) with the ‘PhyloClim’ package (Heibl & Calenge 2011). The value of D ranges between 0, when two species/gene pools have no niche overlap, and 1, when the two species/gene pools share the same environmental space.

To evaluate niche conservatism between related species and gene pools, two randomization tests were run: the niche identity test and the niche similarity test (the latter is also called “background test”, Warren et al. 2008). For the identity tests, 100 pseudoreplicates were created from the pooled localities for each pair of species/gene pool and D values were calculated for each of the pseudoreplicate models. The distribution of these values was then compared to the D values calculated from the actual niche models for that species/gene pool pairs in the niche overlap test. The null hypothesis is that the two species/gene pools have equivalent ecological niches and is expected to be met only if both species/gene pool tolerate exactly the same environmental conditions and have an equivalent set of environmental condition available to them (Warren et al. 2008).

The similarity test allows testing for niche conservatism or divergence that cannot be explained by regional similarities or differences in the habitat available to each species or gene pool (Warren et al. 2008). For each species/gene pool pair, the niche model for the focal species/gene pool is compared to a series of pseudoreplicate models generated by randomly sampling the available habitat (also called the “background”) of its related species/gene pool. The distribution of the D values calculated for each pseudoreplicate model was compared to the D value calculated for the actual data. The available habitat of a species/gene pool is defined as the area that is within the dispersal capabilities, either in the present day or through the relevant past (Peterson 2011). To approximate the available habitat, we used a set of circular buffers of increasing diameters around occurrence data (50, 100 and 200 km around occurrence data for species and 25, 50, and 100 km around occurrences data for gene pools with R package ‘rgeos’, Bivand & Rundel 2014). The null hypothesis of the similarity test is that measured niche overlap between species or gene pools is explained by regional similarities or differences in available habitat. Rejection of the null hypothesis indicates that the observed niche differentiation between species or gene pools is a function of habitat selection rather than simply an artifact of the environmental differences between the available habitats (Warren et al. 2008).

RESULTS

Potential distribution of *Erythrophleum* species and gene pools

For all distribution models, at the species and at the gene pool level, the discrimination between environmental conditions of occurrence localities from those of background localities was good (table 1). For evaluating the robustness of

Table 1 – Performance of SDMs selected based on AIC for each *Erythrophleum* species and gene pool.

Five indicators were used to assess the SDM performance. Abbreviations correspond to AUC_{test}: Area Under the receiver operating characteristic Curve calculated with a test sample; AUC_{diff}: the difference between AUC values based on training localities and AUC_{test}; OR_{mtp}: the Minimum Training Presence Omission Rate; TSS: the True Skill Statistic. The feature class is given for each SDM with abbreviations corresponding to L: linear, Q: quadratic, H: hinge. RM corresponds to the Regularization Multiplier. For gene pools, abbreviations correspond to: *E. ivo W*: West Africa *E. ivorensis*; *E. ivo Cn*: northern Central Africa *E. ivorensis*; *E. ivo Cs*: southern Central Africa *E. ivorensis*; *E. sua W*: West Africa *E. suaveolens*; *E. sua Cn*: northern Central Africa *E. suaveolens*; and *E. sua Cs*: southern Central Africa *E. suaveolens*.

	Species			Gene pools				
	<i>E. ivorensis</i>	<i>E. suaveolens</i>	<i>E. africanum</i>	<i>E. ivo Cs</i>	<i>E. ivo Cn</i>	<i>E. sua Cs</i>	<i>E. sua Cn</i>	<i>E. sua W</i>
FC	LQ	LQ	LQ	LQ	LQH	LQHP	LQ	LQ
RM	0.5	2.5	6	1	3	1	1	6
AUC _{test}	0.94	0.71	0.71	0.91	0.84	0.78	0.90	0.91
AUC _{diff}	0.03	0.06	0.07	0.05	0.06	0.08	0.02	0.01
OR _{mtp}	0.05	0.03	0.01	0.16	0.06	0.12	0.09	0.08
TSS	0.93	0.44	0.33	0.64	0.78	0.52	0.83	0.87

an ENM, AUC values greater than 0.9 are considered to be “very good” at describing a population’s distribution, while AUC values of 0.7–0.9 are considered to be “good”, and less than 0.7 are classified as being “uninformative” (Baldwin 2009). Here, the AUC values for all models ranged from 0.71 to 0.94 (four models with an AUC equal or higher than 0.90). Examination of TSS values also yielded high predictive accuracies. AUC_{diff} and OR_{MTP} values were low (range of 0.01 to 0.08 and 0.01 to 0.16, respectively) indicating relatively few model overfittings. The features of the selected models were mostly linear and quadratic (table 1).

At the species level, the modelled potential distribution for each species accurately predicted the observed species’ distribution (fig. 2A). The potential distribution of *E. ivorensis* was restricted to the evergreen forests in the Upper and Lower Guinean Subcentres and thus showed an interruption in the Dahomey gap. *Erythrophleum suaveolens* had a wide potential distribution that extended over the entire Guineo-Congolian Centre, with the exception of the area occupied by *E. ivorensis*, and the adjacent Transition Zones (Guineo-Congolian/Zambeian and the Guineo-Congolian/Sudanian). The model did not predict a high probability of presence of *E. suaveolens* in the Zambeian Centre except in southern Tanzania and northern Mozambique. The potential distribution of *E. suaveolens* was also largely distinct from that of *E. africanum* except in the Guineo-Congolese/Sudanian and Guineo-Congolese/Zambeian Transition Zones where the distributions overlapped. The potential distribution of *E. africanum* was restricted to the savannas of the Sudanese and Zambeian Centres and to the Transition Zones around the Guineo-Congolian Centre.

At the gene pool level, the models suggest overlapping potential distributions for the *E. ivorensis* gene pools (fig. 2B) but distinct potential distributions for the *E. suaveolens* gene pools (fig. 2C). The *E. ivo Cn* potential distribution covered almost the whole distribution of *E. ivorensis* and extended to the geographic area occupied by *E. ivo W*. The potential distribution of *E. ivo Cs* was restricted to the low coastal plain of the Gabon estuary with a relative low probability of pres-

ence that extended along the coast. The potential distributions of *E. sua W*, *E. sua Cn* and *E. sua Cs* were largely distinct (fig. 2C). *E. sua W* spanned the Upper Guinean Subcentre, the Dahomey Gap and the northern part of the Lower Guinean Subcentre. In central Africa, the potential distribution of *E. sua Cn* was mainly localized in south east Cameroon whereas *E. sua Cs* was restricted to Gabon and Republic of the Congo.

Climatic constraints on the distribution of *Erythrophleum* species and gene pools

The distribution of the three *Erythrophleum* species was mainly constrained by annual precipitation, annual temperature range, precipitation of driest quarter and altitude (table 2 and electronic appendix 2). Annual precipitation and annual temperature range explain together more than 40% of the distribution of each species (table 2). Overall, *E. suaveolens* and *E. africanum* were found in the same range of annual precipitation (optimum close to 1690 mm for *E. suaveolens* and 1700 mm for *E. africanum*), whereas *E. ivorensis* was found at higher annual precipitation (optimum close to 3900 mm). *Erythrophleum ivorensis* and *E. suaveolens* showed an optimum suitability at low annual temperature range (close to 8°C) while *E. africanum* occurs in sites with high annual temperature range (close to 30°C, table 2). The distribution of *E. ivorensis* and *E. suaveolens* was also constrained by elevation and showed an optimum at relatively low altitudes (between 0 and 400 m). Precipitation of the driest quarter was an important constraint on the distribution of *E. africanum* with highest suitability at values close to 0 mm, corresponding to an extreme dry season (table 2).

In the Upper and Lower Guinean Subcentres, the distribution of *E. ivorensis* and *E. suaveolens* gene pools showed contrasting responses to the environment (table 2, electronic appendix 2). Precipitation of the warmest quarter was the most important constraint on the potential distribution of *E. ivo Cs* and *E. sua W* (64.7% and 80.7% respectively with high permutation values) and to a lesser extent on the distri-

Table 2 – Contribution (C in %) and permutation (P in %) of the eight retained environmental variables to model the distribution of each species and gene pool.

A very low percentage of permutation indicates that the model did not depend heavily on the variable. For each species/pool, the three most important environmental variables, i.e. with highest contribution and with a permutation score at least 5%, are shown in bold. For gene pools, abbreviations correspond to: *E. ivo W*: West Africa *E. ivorensis*; *E. ivo Cn*: northern Central Africa *E. ivorensis*; *E. ivo Cs*: southern Central Africa *E. ivorensis*; *E. sua W*: West Africa *E. suaveolens*; *E. sua Cn*: northern Central Africa *E. suaveolens*; and *E. sua Cs*: southern Central Africa *E. suaveolens*.

Environmental variables	Species				Gene pools			
	<i>E. ivorensis</i>	<i>E. suaveolens</i>	<i>E. africanum</i>	<i>E. ivo Cs</i>	<i>E. ivo Cn</i>	<i>E. sua Cs</i>	<i>E. sua Cn</i>	<i>E. sua W</i>
Annual mean temperature	C = 0.0	C = 5.3	C = 0.0	C = 0.3	C = 0	C = 1.5	C = 3.2	C = 0
	P = 5.3	P = 11.0	P = 0.0	P = 0	P = 0	P = 11.1	P = 18.6	P = 0
Isothermality	C = 0.3	C = 0.0	C = 0.2	C = 0	C = 0	C = 3.5	C = 40.3	C = 0
	P = 2.5	P = 0.0	P = 5.1	P = 0	P = 0	P = 4.8	P = 0	P = 0
Annual temperature range	C = 33.0	C = 33.9	C = 26.3	C = 26	C = 36	C = 7.5	C = 0	C = 0
	P = 13.1	P = 12.8	P = 31.3	P = 43.3	P = 46.5	P = 3.2	P = 0.7	P = 0
Annual precipitation	C = 29.9	C = 23.9	C = 18.1	C = 2.3	C = 17.2	C = 0.6	C = 17.5	C = 0
	P = 40.9	P = 32.7	P = 18.4	P = 0	P = 5	P = 3.8	P = 33	P = 0
Precipitation seasonality	C = 3.6	C = 4.0	C = 0.2	C = 0	C = 0.2	C = 1.2	C = 22.9	C = 0
	P = 7.8	P = 6.2	P = 0.2	P = 0	P = 0	P = 4.4	P = 29	P = 0
Precipitation of driest quarter	C = 1.4	C = 0.5	C = 50.1	C = 0	C = 27.1	C = 0.9	C = 3.5	C = 19.3
	P = 6.7	P = 2.7	P = 42.2	P = 0	P = 0	P = 0	P = 1.9	P = 39.7
Precipitation of warmest quarter	C = 16.1	C = 6.0	C = 3.5	C = 64.7	C = 0	C = 15.5	C = 2.5	C = 80.7
	P = 0.4	P = 9.0	P = 2.8	P = 32.3	P = 0	P = 26.7	P = 4.7	P = 60.3
Precipitation of coldest quarter	C = 2.9	C = 1.4	C = 0.6	C = 0	C = 8.4	C = 62.2	C = 0.5	C = 0
	P = 3.3	P = 0.2	P = 0.0	P = 0	P = 29.4	P = 40	P = 6	P = 0
Elevation	C = 12.8	C = 25.0	C = 1.0	C = 6.6	C = 11.2	C = 7	C = 9.6	C = 0
	P = 20.1	P = 25.3	P = 0.0	P = 24.4	P = 19.1	P = 6.1	P = 6.1	P = 0

bution of *E. sua Cs* (15.5%; table 2). The presence probability of *E. ivo Cs* and *E. sua Cs* increased with precipitation of the warmest quarter (respectively optimum close to 1070 mm and optimum when Bio18 was superior to 570 mm) while the probability of *E. sua W* decreased (optimum close to 65 mm). Annual temperature range was an important environmental factor constraining the distribution of both *E. ivo Cs* and *E. ivo Cn* (respectively 26% and 36% of contribution, table 2) with highest suitability at values close to 8°C (electronic appendix 2). The precipitation seasonality (22.9%) and annual precipitation (17.5%) together shape the potential distribution of *E. sua Cn* (table 2). Areas with precipitation seasonality around 20 mm and with an annual precipitation of 850 mm showed highest suitability.

Niche overlap and conservatism among *Erythrophleum* species and gene pools

Pairs of species/gene pools showed varying degrees of niche overlap, from limited overlap (D = 0.09) between *E. sua W* and *E. sua Cn* to high overlap (D = 0.53 and 0.47) between *E. ivo Cn* and *E. ivo Cs*, and between *E. suaveolens* and *E. africanum* (table 3).

For all the species and gene pool pairs, the null hypothesis of the identity test (p < 0.001) was rejected. The species/gene pools did not tolerate exactly the same environmental conditions and/or had not equivalent set of environmental conditions available to them. Although these results could reflect ecological divergence, they might also simply reflect the fact that species/gene pools are exposed to different available habitats.

The null hypothesis of the similarity test was rejected at species level and for the *E. suaveolens* gene pools (table 3), thus indicating that the observed niche differentiation between the species and the *E. suaveolens* gene pools was a function of habitat selection rather than simply an artifact of the environmental differences between the available habitats. On the contrary, the similarity tests indicated that the niche of the *E. ivorensis* gene pools tended to be more similar than expected by chance and provided an evidence for niche conservatism (table 3). One comparison shifted from similar to divergent niches with buffer size: the niche of *E. sua W* vs. *E. sua Cn* were significantly more similar until the 50 km scale, but significantly less similar at the 100 km scales (table 3).

DISCUSSION

In Africa, only few studies characterized the relationship between the distribution of sister plant species and climate (but see Dransfield & Uhl 2008, Blach-Overgaard et al. 2010, Holstein & Renner 2011, Couvreur et al. 2011). Studies on intra-specific diversity are even less common. Here, we explored the role of ecology into diversification of the *Erythrophleum* genus in tropical Africa. We specifically investigated the climatic constraints on the distribution at the species and gene pool levels. At the species level, our results provide baseline evidence to support a case of climate-driven ecological speciation. At the gene pool level, past climate changes during the Pleistocene have probably shaped genetic

diversity, though within *E. suaveolens*, adaptive divergence most probably also occurred.

Ecological speciation has probably played a key role in the evolution of African *Erythrophleum* species. Climatic niches of the related species tended to be less similar than expected by chance and provided evidence for adaptive divergence (Graham et al. 2004, Warren et al. 2008). The climate, and specifically annual precipitation and annual temperature range, strongly constrained the distribution of the species and our results confirmed the affinity of *E. ivorensis* for wet forest conditions, the huge ecological amplitude of *E. suaveolens* across moist and dry forests, and the association of *E. africanum* with savannas. The traits and growth rates previously observed among *Erythrophleum* species are consistent with an ecological sorting along an aridity gradient. The savanna species, *E. africanum*, associated with the driest habitats, has the smallest leaves (6.5×3.5 cm), the highest wood density (0.852 ± 0.036 g/cm³) and the lowest growth rates (0.15 cm/year, see Gorel et al. 2015 for a review on *Erythrophleum* species in Africa). These traits characterize drought-tolerant tropical tree species (Markesteyn & Poorter 2009). In contrast, the wet forest species, *E. ivorensis* shows the opposite suite of traits and the highest growth rates (leaves: 8.5×4 cm; wood density: 0.774 ± 0.058 g/cm³; growth rates: 0.65 ± 0.50 cm/year).

The climate-constrained distribution of the species associated with the estimated divergence dates (Duminil et al. 2015) argue for past climate changes promoting ecological speciation. Past climate changes are expected to fa-

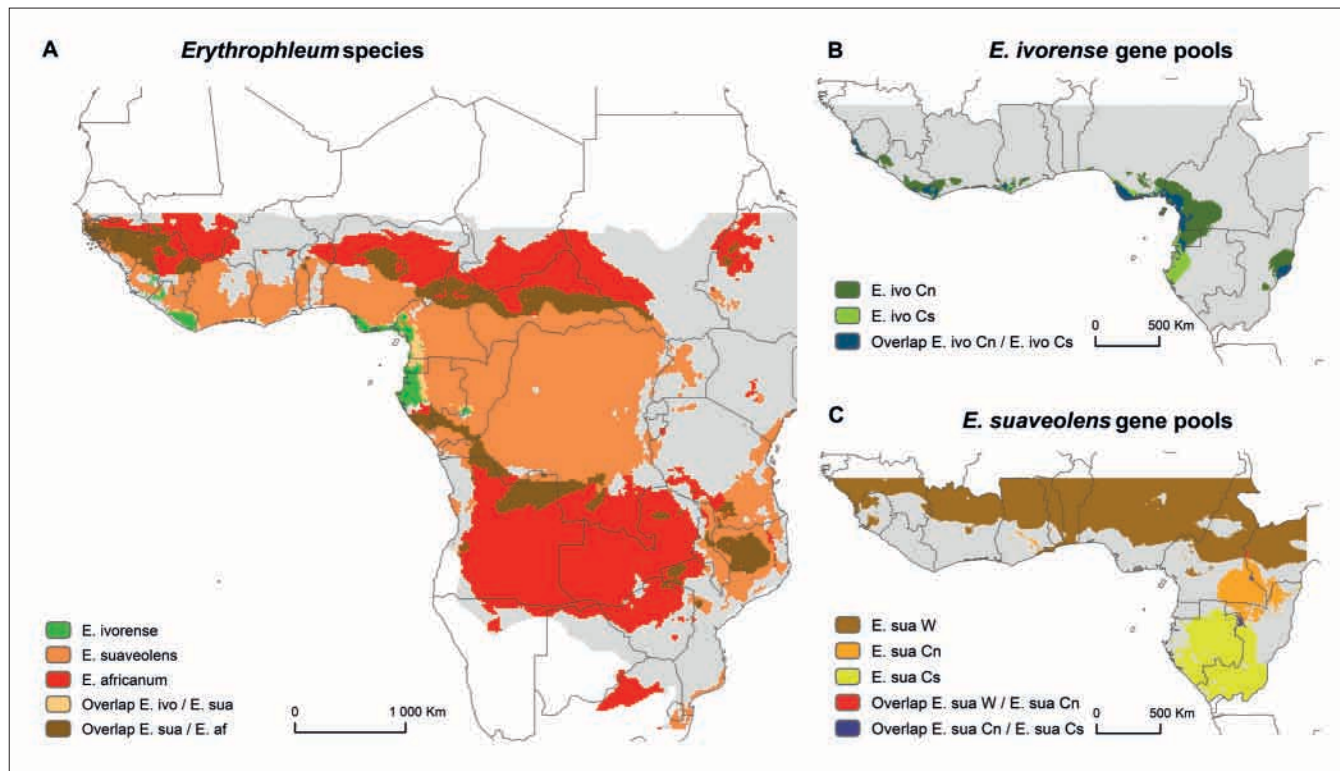


Figure 2 – Potential distributions for *Erythrophleum* species (A), *E. ivorensis* (B) and *E. suaveolens* gene pools (C). Suitable areas were identified for the three species and the five gene pools using a suitability threshold that was identified by maximizing the sum of the sensitivity (true positive rate) and specificity (true negative rate). Overlap between pairs of species and pools are also given.

Table 3 – Niche overlap and similarity between pairs of *Erythrophleum* species and gene pools.

Niche overlap (D) and results of the similarity tests with P-values (P) are given for each species pair and for different background definitions (25, 50, 100 and 200 km buffers). D is the Schoener's D similarity metric. Dcomp is the Schoener's D metric calculated to compare the overlap between the SDM of each species and its own null model, which illustrate how environmental heterogeneity increases with the distance of occurrence points for each species (for the method see Nakazato et al. 2010). For gene pools, abbreviations correspond to: *E. ivo W*: West Africa *E. ivorensis*; *E. ivo Cn*: northern Central Africa *E. ivorensis*; *E. sua W*: West Africa *E. suaveolens*; *E. sua Cn*: northern Central Africa *E. suaveolens*; and *E. sua Cs*: southern Central Africa *E. suaveolens*. More/less similar indicate that niches are more/less similar than expected by chance (null model). ns: not significant ($P > 0.05$).

	25 km buffer		50 km buffer		100 km buffer		200 km buffer	
	D _{comp}	Similarity	D _{comp}	Similarity	D _{comp}	Similarity	D _{comp}	Similarity
<i>E. ivorensis</i> – <i>E. suaveolens</i> (Null)	–	–	0.90 ± 0.01	Less similar $P <= 0.001$	0.85 ± 0.01	Less similar $P <= 0.001$	0.81 ± 0.01	Less similar $P <= 0.05$
<i>E. suaveolens</i> – <i>E. ivorensis</i> (Null)	–	–	0.79 ± 0.01	Less similar $P <= 0.001$	0.69 ± 0.01	Less similar $P <= 0.001$	0.59 ± 0.01	Less similar $P <= 0.001$
<i>E. suaveolens</i> – <i>E. africanum</i> (Null)	0.47	–	0.86 ± 0.02	Less similar $P <= 0.001$	0.84 ± 0.02	Less similar $P <= 0.001$	0.80 ± 0.03	Less similar $P <= 0.001$
<i>E. africanum</i> – <i>E. suaveolens</i> (Null)	–	–	0.88 ± 0.02	Less similar $P <= 0.001$	0.87 ± 0.02	Less similar $P <= 0.001$	0.82 ± 0.03	Less similar $P <= 0.001$
<i>E. ivo Cs</i> – <i>E. ivo Cn</i> (Null)	0.53	More similar $P <= 0.001$	0.54 ± 0.01	More similar $P <= 0.001$	0.57 ± 0.01	More similar $P <= 0.001$	–	–
<i>E. ivo Cn</i> – <i>E. ivo Cs</i> (Null)	–	More similar $P <= 0.001$	0.49 ± 0.01	More similar $P <= 0.001$	0.49 ± 0.02	More similar $P <= 0.001$	–	–
<i>E. sua Cs</i> – <i>E. sua Cn</i> (Null)	0.26	ns	0.65 ± 0.01	ns	0.61 ± 0.01	Less similar $P <= 0.001$	–	–
<i>E. sua Cn</i> – <i>E. sua Cs</i> (Null)	–	Less similar $P <= 0.001$	0.80 ± 0.01	Less similar $P <= 0.001$	0.79 ± 0.01	Less similar $P <= 0.001$	–	–
<i>E. sua W</i> – <i>E. sua Cn</i> (Null)	0.09	More similar $P <= 0.001$	0.66 ± 0.01	More similar $P <= 0.001$	0.65 ± 0.01	Less similar $P <= 0.001$	–	–
<i>E. sua Cn</i> – <i>E. sua W</i> (Null)	–	More similar $P <= 0.001$	0.52 ± 0.02	More similar $P <= 0.001$	0.56 ± 0.03	ns	–	–

your adaptive divergence by driving reproductive isolation between fragmented populations in distinct environments (Rundle & Nosil 2005, Nosil 2012) or also, in the case of new climates moving as a front across landscapes, by increasing the opportunity of individuals to adapt to new conditions (Donoghue & Edwards 2014). For these reasons, the slightly warmer climates of the early Pliocene (until ~3.2 Ma, Zachos et al. 2001) could have boosted the divergence of *E. africanum* from the common ancestor of *E. suaveolens* and *E. ivorensis*. Between *E. suaveolens* and *E. ivorensis*, the divergence date is concomitant with the Pleistocene climatic cycles (c. 650 ka, Duminil et al. 2015) *i.e.* the climate-driven contractions of forests inside refuges. Speciation between the two forest species is probably due to the combined action of the isolation of populations into forest refuges and the adaptation to contrasting environments (Vanzolini & Williams 1981, Damasceno et al. 2014).

Within species, the gene pools are distributed in contrasted climate for *E. suaveolens*, and at contrasted altitude for *E. ivorensis* (electronic appendix 2), however, a general conclusion on the role of ecology into genetic diversification is more difficult to picture out. The climate-driven contractions of forests inside refuges during the Pleistocene have probably shaped intra-species genetic diversity (Hardy et al. 2013, Duminil et al. 2015), though within *E. suaveolens*, adaptive divergence also occurred. Within *E. suaveolens*, the climatic niches of the gene pools tended to be less similar than expected by chance, providing evidence for ecological divergence (Graham et al. 2004, Warren et al. 2008). *E. suaveolens* gene pools are distributed along rainfall gradients: at one end, the West African gene pool (*E. sua W*), is found in the more arid habitats, and at the other end the southern gene pool (*E. sua Cs*) occupied higher rainfall habitats. In northern Cameroon, the genetic discontinuity between the Central and the West African gene pools of *E. suaveolens* is located between the Guineo-Congolian Centre and the Guineo-Congolian/Sudanian Transition Zone (White 1983) and corresponds to a steep ecological transition. The northern limit of the southern gene pool (*E. sua Cs*) correspond to the climatic hinge as defined by Suchel (1990), where the sunny dry season in the north and the cloudy one in the south (Philippon et al. accepted 2018), less harsh for plants, have already been hypothesized as driver of floristic diversification (Suchel 1990, Gonmadje et al. 2012). We noted that, according to the similarity tests, the *E. sua W* vs. *E. sua Cn* niche comparison shifted from similar to divergent with buffer size. At fine and medium scales, the two gene pools occupy similar habitats, but at larger scales (100 km buffer size) the available habitat is more suitable for *E. sua W* than the locations where *E. sua Cn* is found and *vice versa*. This result may be explained by the poor resolution of the bioclim variables at a local scale (< 50 km) which may be not sufficient to discriminate between the two habitats (Deblauwe et al. 2016). This might also indicate significant niche divergence, contingent upon the assumption that 100 km is a reasonable estimate of the dispersal potential of *E. suaveolens* over the relevant past period (perhaps since the last glacial episode c. 115–10 ka, Peterson 2011).

Within *E. ivorensis*, the similarity tests support niche conservatism, rejecting ecological divergence and supporting the

forest refuge hypothesis. Interestingly, the genetic differentiation within *E. ivorensis* has been identified to be lower than the genetic differentiation within *E. suaveolens* (Duminil et al. 2013, 2015). To interpret these results, Duminil et al. (2015) suggested that the distribution of *E. ivorensis* has been less fragmented than that of *E. suaveolens*, either because glacial refugia of *E. ivorensis* were closer to each other and/or were separated for a shorter period than that of *E. suaveolens*. The uniform environmental conditions occupied by the gene pools of *E. ivorensis* can also be an alternative explanation to the lower genetic differentiation. *E. ivorensis* is a wet-forest specialist while *E. suaveolens* is more generalist, distributed across multiple environments. Indeed, specialist species are more likely to suffer from resources limitation and are more susceptible to environmental changes and local extinction during climate changes (Sexton et al. 2017). *Erythrophleum ivorensis* may have been able to survive only in a very narrow range of environmental conditions during past forest fragmentation (*i.e.* in environmentally similar refuges) and isolated populations were therefore not been subjected to divergent selection. In contrast, the huge ecological amplitude of *E. suaveolens* could have contributed to the survival of populations inside refuges with distinct environmental conditions, as shown by Rolland & Salamin (2016) for animals and theoretically developed by Sexton et al. (2017). Then, divergent selection induced local adaptation and genetic diversification between populations, which was boosted by the absence of gene flow due to spatial isolation (Rundle & Nosil 2005).

Ecological speciation along rainfall gradients is probably a key mechanism in the diversification of the tropical African flora, since equivalent patterns of niche partitioning exist within many other genera, such as *Diospyros* (White 1978), *Azelia* (Donkpegan 2017) and *Guibourtia* (Tosso 2018). At the intra-species level, though we believe that the *E. suaveolens* gene pools in the Upper and Lower Guinean Subcentres grow under strongly different environmental conditions, the expanding distribution of gene pools recolonizing from different forest refugia might have obscured the similarity tests (Graham et al. 2004, Guisan & Thuiller 2005). In contrast, niche conservatism can be found potentially due to the fact that a crucial ecological dimension was not included among variables tested (Graham et al. 2004, Guisan & Thuiller 2005). Defining niches along relevant environmental axes is a challenge and our results strongly depend on the environmental factors we have tested. For instance, even if climate and specifically rainfall has been found as a main driver of floristic diversity in multiple studies (Engelbrecht et al. 2007, Maharjan et al. 2011, Sterck et al. 2014, Gaviria et al. 2017), conclusions about the role of climate in the diversification processes within *Erythrophleum* may be confounded by the correlations between climate and other environmental factors, as soil fertility (Swaine 1996) and mycorrhizal association (Gerz et al. 2018). To valid ecological divergence between the species and gene pools, additional observations on their differential abilities to survive and reproduce in different local environmental conditions, possibly including the experimental quantification of drought tolerance, would be useful (Engelbrecht et al. 2007).

SUPPLEMENTARY DATA

Supplementary data are available in pdf at *Plant Ecology and Evolution*, Supplementary Data Site (<https://www.ingentaconnect.com/content/botbel/plecevo/supp-data>) and consist of: (1) Pearson correlation coefficients between the 19 Bioclim variables and the altitude; and (2) response curves to the 8 retained environmental variables for each species, *E. ivorensis* gene pools and *E. suaveolens* gene pools.

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