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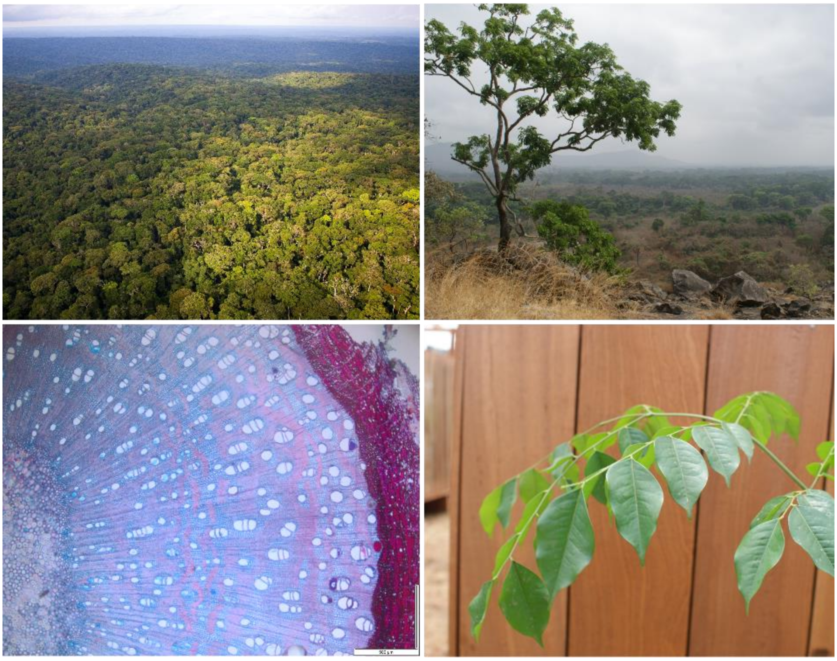
Anaïs-Pasiphaé Gorel



COMMUNAUTÉ FRANÇAISE DE BELGIQUE
UNIVERSITÉ DE LIÈGE – GEMBLOUX AGRO-BIO TECH

CLIMATIC NICHE EVOLUTION WITHIN TROPICAL TREE LINEAGES: THE CASE OF THE *ERYTHROPHLEUM* GENUS (FABACEAE - CAESALPINIOIDEAE) IN AFRICA

Anaïs-Pasiphaé Gorel

Dissertation originale présentée en vue de l'obtention du grade de docteur en sciences agronomiques et ingénierie biologique

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Abstract

In Africa, while some plant groups and specifically genera are strictly associated to specific biomes, evidence of widely distributed genera transcending biome or habitat boundaries have also been reported for herbaceous plants and for tree genera. In this thesis, we aim at understanding the evolutionary processes that allowed particular tropical tree lineages to adapt to contrasted environmental conditions and occur in vast areas. While a diversity of methods at different phylogenetic and spatial scales can provide complementary insights, detailed analyses of well-resolved clades are needed to build robust generalizations about niche evolution and biome shifts. Therefore, from species distribution modeling to hard physiological measurements, we attempt to disentangle the processes explaining the vast distribution of *Erythrophleum* (Fabaceae), a tropical tree genus widely distributed in Africa, Australia and China.

A synthesis is first provided on the *Erythrophleum* species in Africa (**Chapter 2**). *Erythrophleum* encompasses two forest species and two savanna species. The forest species are morphologically similar and sold for timber under the same commercial name, Tali, but genetics revealed contrasted distribution. *Erythrophleum ivorense* is restricted to the wet coastal forest, while *Erythrophleum suaveolens* occurs over vast areas from the moist forest up to gallery forests in the savanna.

Secondly, we use species distribution models to determine the bioclimatic constraints on the distribution of the *Erythrophleum* species and gene pools (**Chapter 3**). Our results support the substantial role of climate in niche evolution, and speciation, within the genus. *Erythrophleum* has managed to adapt to extremely contrasted climates, resulting in a distribution encompassing several biomes, from the wet forest to the dry forest and the savanna.

Ecophysiological (**Chapter 4**) and experimental (**Chapter 5**) approaches are then used to get a functional understanding of the niche evolution within *Erythrophleum*. We find that, for the two forest species, the shift into drier environments was associated with a coordinated evolution of the xylem resistance to embolism, controlled by subtle adaptations in wood anatomical traits, and desiccation delay strategies at stem and leaf levels.

Finally, after confronting our results with previous studies on congeneric species, we conclude that, for certain tree lineages, the lability of drought tolerance traits, specifically those related to xylem protection, is an important functional path allowing to transcend habitat and biome boundaries (**Chapter 6**). We then discuss the generalization of the niche evolution pattern we detected for *Erythrophleum* to other African genera. Comparing the niche of 1439 woody species at the continental scale, we provide new evidence supporting the niche evolution within many woody genera in tropical Africa (20% of the 532 studied genera).

Résumé

En Afrique, alors que certains genres de plantes sont strictement limités à un biome, d’autres sont plus largement répandus. L’objectif de cette thèse est de comprendre les processus évolutifs qui ont permis à ces lignées de s’adapter à des conditions variées, et ainsi, de transcender les frontières des habitats. Bien que de nombreuses méthodes à différentes échelles phylogénétiques et spatiales puissent fournir des informations complémentaires, l’analyse détaillée de genres dont la phylogénie est connue est nécessaire pour comprendre les mécanismes d’évolution de niche. Par l’utilisation de modèles de distribution jusqu’à de fines mesures écophysiologiques, nous avons identifié les processus évolutifs associés à la distribution d’*Erythrophleum*, un genre d'arbres tropicaux largement répandu en Afrique, en Australie et en Chine.

Dans un premier temps, nous avons réalisé une synthèse des données concernant les espèces africaines du genre (**Chapitre 2**). Le genre *Erythrophleum* comprend deux espèces de forêt, morphologiquement similaires et commercialisées sous le même nom : Tali. Des études génétiques ont révélé que ces deux espèces occupent des zones contrastées. *Erythrophleum ivorense* est inféodé aux forêts humides sempervirentes côtières alors qu’*Erythrophleum suaveolens* est présent des forêts semi-décidues jusqu’aux galeries forestières au sein des savanes. Le genre *Erythrophleum* comprend également deux espèces de savane : *Erythrophleum africanum* très largement distribué en Afrique et *Erythrophleum lasianthum* restreint au nord du Mozambique.

Dans un second temps, nous avons utilisé des modèles de distribution pour identifier les variables bioclimatiques qui structurent la distribution des espèces et des populations génétiques en Afrique (**Chapitre 3**). Nos résultats ont confirmé le rôle important du climat dans l'évolution de la niche et la spéciation au sein du genre. *Erythrophleum* s’est adapté à différents régimes de précipitation, ce qui explique sa distribution englobant les biomes, de la forêt humide à la forêt sèche jusqu’à la savane.

Nous avons ensuite utilisé des approches écophysiologiques (**Chapitre 4**) et expérimentales (**Chapitre 5**) afin d'obtenir une compréhension fonctionnelle de l'évolution de la niche d'*Erythrophleum*. Pour les deux espèces forestières, la colonisation de milieux secs est associée à l'évolution de la résistance à l’embolisme et de stratégies de retard de dessiccation. Ces résultats confirment que la labilité des traits associés à la tolérance à la sécheresse, en particulier les traits liés à la sécurité du xylème, est une voie fonctionnelle importante permettant aux lignées de transcender les frontières des biomes (**Chapitre 6**).

Finalement, la généralisation des patrons d’évolution de niche détectés pour *Erythrophleum* à d'autres genres africains a été examinée. En comparant la niche de 1439 espèces ligneuses à l’échelle continentale, nous avons pu mettre en évidence une évolution de niche au sein de nombreuses genres ligneux en Afrique tropicale (20% des 532 genres étudiés ; **Chapitre 6**).

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Abbreviations

$\delta^{18}O$:	Ratio of stable isotopes oxygen-18 (^{18}O) and oxygen-16 (^{16}O).
^{14}C:	Radiocarbon
A:	Photosynthetic rate (µmol/m^2/s)
AE:	Acoustic emission
$AE_{12,\ 50,\ 88,\ 100}$:	The water potential at which the xylem experiences 12, 50, 88 and 100 % loss of conductivity assessed with the acoustic emission method
af:	*Erythrophleum africanum*
AIC:	Akaike information criterion
AUC:	Area Under the Curve
BP:	Before present (i.e. before 1950)
CEI_{juv}:	Crown exposure index at 10 cm DBH
C_{el}:	Elastic capacitance
C_{inel}:	Inelastic capacitance
D:	Schoener's D metric
DBH:	Diameter at Breast Height
DOY:	Day Of Year
E:	Transpiration rate (mmol/m^2/s)
g_s:	Stomatal conductance (mmol/m^2/s)
ivo:	*Erythrophleum ivorense*
ka:	Thousand years
O:	Niche overlap
PCA:	Principal Component Analysis
PNC:	Phylogenetic Niche Conservatism
PND:	Phylogenetic Niche Divergence
PPFD:	Photosynthetic Photon Flux Density (µmol/m^2/s^2)
SDM:	Species Distribution Model
SE:	Standard Error
sua:	*Erythrophleum suaveolens*
SWC:	Soil Water Content
VC:	Vulnerability Curve
VC_{AE}:	Acoustic Vulnerability Curve
WC:	Water Content
VWC:	Volumetric Water Content
WS:	Witling stage
π_{TLP}:	Water potential at the turgor loss point (MPa)
Ψ:	Water potential (MPa)
$\Psi_{12,\ 50,\ 88,\ 100}$:	The water potential at which the xylem experiences 12, 50, 88 and 100 % loss of conductivity

1

General introduction

1 The spatial patterns of vegetation and climate

1.1 The global distribution of biomes

At least on land, plants shape and dominate biotic communities. These communities are structured along temporal and spatial scales. Identifying and mapping these structures is a keystone in ecology because it enables the study of the underlying biogeographical, evolutionary and ecological processes involved in their assembly (Schimper 1903, Holdridge 1947, Whittaker 1970, Walter 1973, Mucina 2019).

Biogeographic patterns have been defined at various scales and with numerous methods. At very large scale, biomes are the basal vegetation unit commonly used to describe and order biological diversity (**Figure 1.1**). Biomes are defined by structural and functional attributes (Whittaker 1970, Donoghue & Edwards 2014, Moncrieff *et al.* 2015). The assumption behind the biome concept is that, over time, the environment selects and filters organisms, resulting in vegetation units similar in structure and function although geographically and evolutionary distant (Schimper 1903). The biome concept is attractive because it can be applied globally without reference to plant species composition, allowing generality to be sought. Indeed, units compared over a very large distance, e.g. between continents, share few species while the general physiognomy of the vegetation might remain very similar (Mucina 2019).

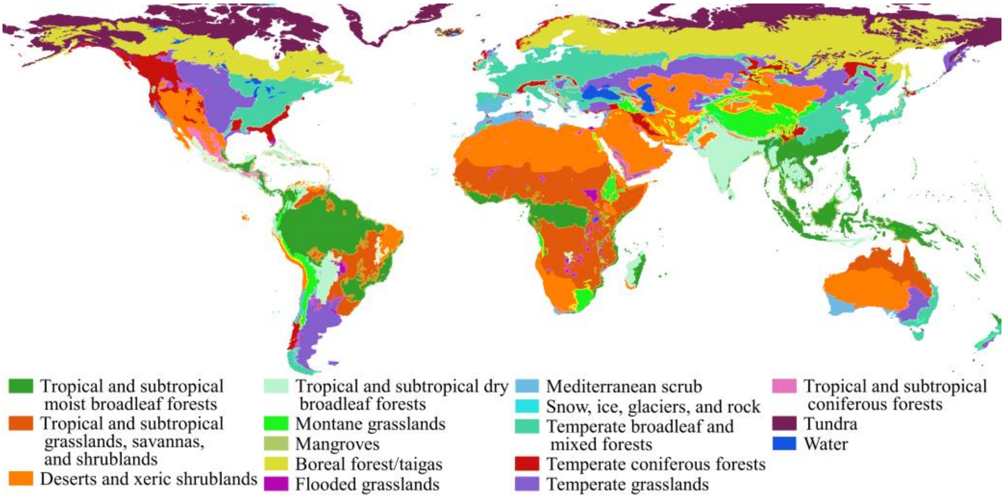

Figure 1.1 Distribution of the world's biomes, from Olson *et al.* (2001) who identified and mapped the World's "Ecoregions".

There is a consensus that biomes are useful for describing the functioning of the world's ecosystems, however, the characterization of the biome categories is still a subject of debate. Due to the latter, a great diversity of maps using different biome characterizations can be found in textbooks. From the fundamental work of Schimper (1903) to the present (Friedl *et al.* 2010), biome delimitation has integrated climatic variables, deviating from the purely functional and physiognomic definition. To tackle this problem, Higgins *et al.* (2016) proposed to map the global terrestrial surface into regions that function similarly using three vegetation attributes: the vegetation height, a vegetation productivity index (VPI) based on the normalized difference vegetation index (NDVI) and a growth limitation index, i.e. a seasonality index which describes whether the lowest point in the annual NDVI cycle corresponds to the driest or the coldest part of the year. A global map of biomes was thus produced (**Figure 1.2**) allowing the analysis of the relationships between biome distribution and climate not confounded by the circularity of using climatic thresholds in the biome definition.

According to the purely structural and functional work of Higgins *et al.* (2016), five major biomes are found in the tropics (**Figure 1.2**). This result contrasts with the dichotomy between tropical and subtropical forest and savanna traditionally recognized, with possibly the inclusion of a third tropical biome: the tropical dry forest (Dexter *et al.* 2018). In the work of Higgins *et al.* (2016), savannas where trees and C4 grasses coexist (Whittaker 1970, Olson *et al.* 2001, Ratnam *et al.* 2011) are subdivided into four different biomes which share growth limitation during the driest part of the year but have contrasting degree of height and vegetation productivity. The tree savanna biome (THD, in red) has tall vegetation and high vegetation productivity. The shrub savannas are characterized by small vegetation and are divided into three distinct biomes based on their vegetation productivity (shrub savanna with high (SHD, in orange), medium (SMD, light orange) and low (SLD, in yellow) vegetation productivity), forming a south-north gradient in West and North Africa. The SLD biome is sparsely vegetated and corresponds to the transition between the shrub savanna and the desert (SLN, sand color). The widespread "tall high VPI non-seasonal" (THN, in green) biome mainly correspond to the wet and moist tropical forests dominated by trees and forming closed canopy and complex vertical structure with C3 grasses in understory.

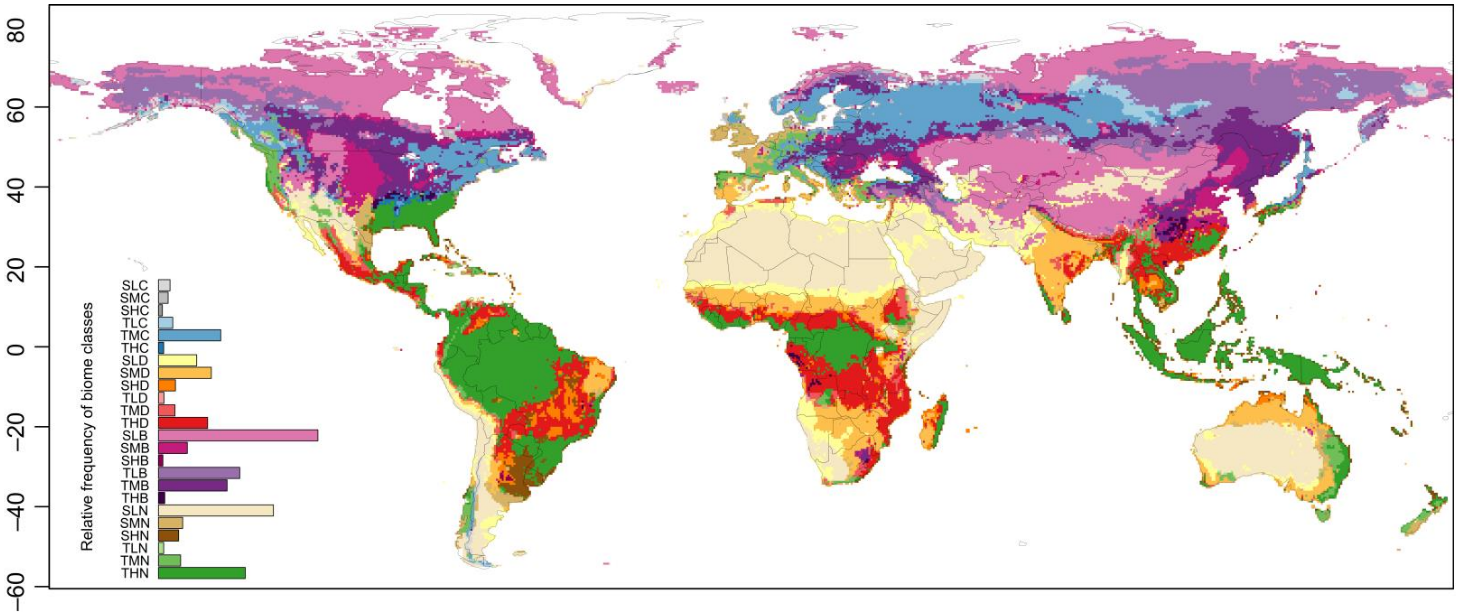

Figure 1.2 Biomes of the world as defined by Higgins *et al.* (2016) based on three vegetation attributes derived from remote-sensing products: the vegetation height, the vegetation productivity index (VPI) and how the vegetation activity is limited by temperature and soil moisture. The biomes shown here are the dominant classification over a 31-year GIMMS3g record. The biome names are derived from three letters (1) “T” or “S” for Tall or Short vegetation height, (2) “L”, “M” or “H” for Low, Medium or High VPI and (3) “C”, “D” or “B” for Cold, Dry or Both cold and dry (nonseasonal) for the growth limitation index.

1.2 The biogeography of Africa

Although useful for global scale comparison, the classification of vegetation on physiognomy brings together floristic units which, in many aspects, are different, and is probably not consistent with the highly complex structural diversity of tropical and subtropical vegetation (White 1983). As one moves down the hierarchy of vegetation types, floristic similarity among the types becomes more informative.

Spatial changes of species composition have been long recognized across tropical Africa (Aubréville 1932, 1962, White 1978, 1983, Denys 1980). Yet, the identification of geographically distinct assemblages of species and communities (*i.e.* the biogeographical regionalization) has been a challenge for over the past century, from the early work of Lebrun (1936) through White (1983), to the more recent studies of Linder *et al.* (2012) for cross-taxonomic comparison and Droissart *et al.* (2018) for plants. The work of White (1979, 1983) currently represents the most widely used chorological and vegetation classification for Africa, and has been validated several times since Denys *et al.* (1980). With the help of a strong botanical expertise, White defined three main types of phytochoria in Africa based on the richness of endemic species: the regional centers of endemism, the transition zones and the regional mosaics (**Figure 1.3a**). A regional center of endemism, such as the Guineo-Congolian, is defined as a phytochorion with both more than 50% of its species confined to it and a total of more than 1000 endemics species. The regional centers of endemism are separated by transition zones which have few endemic species and share the majority of their species with the adjacent phytochoria. Finally, the regional mosaics are more complex phytochoria, formed by an intermingling of physiognomic types with a variability of floristic relationships.

The work of White provided a coherent and useful chorological classification of Africa, however, it remains mostly based on expert's field observation and interpretation of empirical data, limiting reproducibility (Droissart *et al.* 2018). The development of computer-based categorization and the increasing availability of species occurrence databases have opened the way for robust statistical regionalizations of the African flora, leading to reproducible results (Denys 1980, Linder *et al.* 2005, Linder 2014, Droissart *et al.* 2018, Fayolle *et al.* 2014 for forests and Fayolle *et al.* 2018 for savannas). Denys (1980) was the first to employ factorial analysis and distribution of 494 species to undertake an analytical classification of Africa's vegetation, with marked differences between the Guineo-Congolian forest block and the East African vegetation, later confirmed by Fayolle *et al.* (2014). In several studies, Linder *et al.* (2001, 2005, 2012) used ordination and cluster analysis of distribution data to regionalize the African flora objectively. The last study compared plant patterns with those of several groups of vertebrates and found a surprisingly high degree of congruence across groups and a new regionalization of the African biota (**Figure 1.3b**, Linder *et al.* 2012), broadly congruent with the one of White (1983), was proposed.

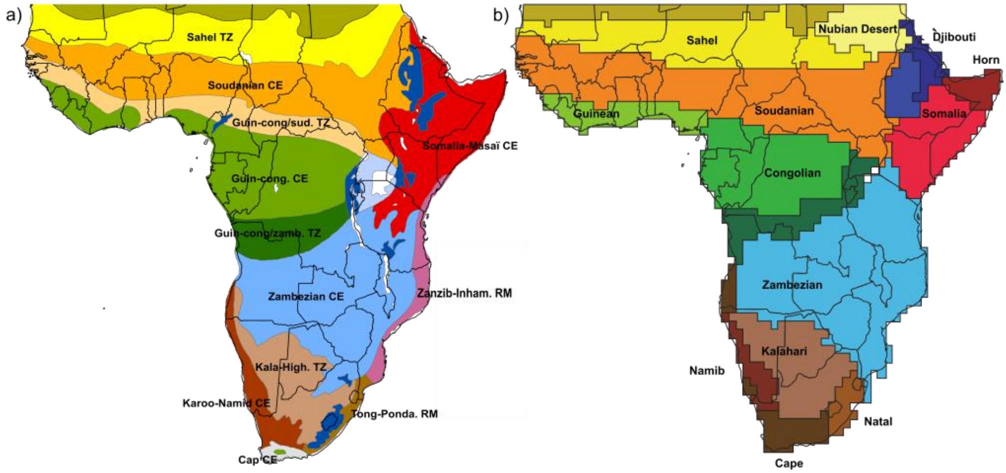

Figure 1.3 Delimitation of the major phytochoria according to (a) White (1983) and (b) Linder (2012). Abbreviations correspond to Centre of Endemism (CE), Regional Mosaic (RM) and Transition Zone (TZ)

In 2018, Droissart *et al.* proposed a biogeographical regionalization of tropical and subtropical Africa based on herbarium records of 24719 plants species (from the RAINBIO dataset, available at http://rainbio.cesab.org/) belonging to four growth forms: terrestrial herbs, trees, shrubs and lianas. Analyzed separately, plant growth forms showed contrasting geographical patterns and the authors concluded that the bioregionalization was better resolved for closed forest types using trees and liana and for open vegetation using terrestrial herbs, while shrubs showed good discriminative power in all vegetation types. When the different growth forms were analyzed together, 16 bioregions and 11 transition zones were identified **(Figure 1.4)**. The delimitation was highly congruent with previous African bioregionalization with clear distinction between the West and Central Africa on one hand and the eastern and the southern Africa on the other.

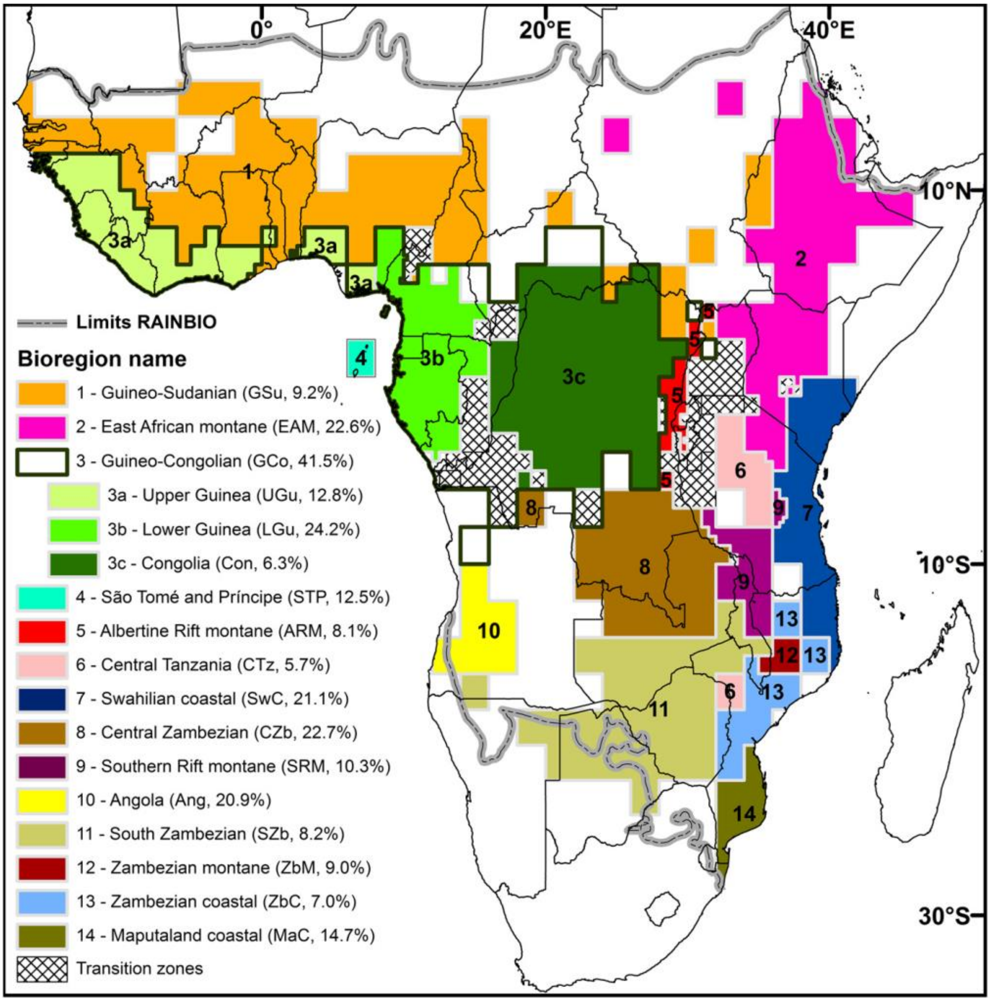

Figure 1.4 The main floristic bioregions and transition zones identified across tropical Africa by Droissart *et al.* (2018) based on herbarium records of 24719 plants species (from the RAINBIO dataset) belonging to four growth forms: terrestrial herbs, trees, shrubs and liana. Only regions with at least 1,000 records are represented. Hatching indicates transition zones, with strict endemism rates lower than 5%. Dashed lines represent the limits for tropical Africa as defined in Droissart *et al.* (2018).

While the majority of the regionalization of African flora was mostly based on herbarium samples or distribution data and might suffer from the false presence artifact in virtual assemblage (Jetz *et al.* 2008), Fayolle *et al.* (2014, 2018), proposed new analyses based on collation of data consisting of the largest collection of localized lists of tree species in tropical African forests (Fayolle *et al.* 2014) and of tree and shrub species in tropical African savannas (Fayolle *et al.* 2018) in order to identify large-scale variation in woody species composition (*i.e.*, beta diversity). For both forests and savannas, the authors identified a major floristic discontinuity between the North/West/Central and the South/East part of Africa (**Figure 1.5a**). This floristic discontinuity closely corresponds to the High and Low division of Africa proposed by White (1983), a line drawn from Angola, then following the Albertine Rift, and then north to the west of Ethiopia (**Figure 1.5a**). Across tropical forests, 6 floristic clusters were identified: Coastal and Upland for East Africa, Dry and Wet-Moist for West Africa, and Moist and Wet for Central Africa (**Figure 1.5a**). Across savannas, eight floristic clusters were identified and in turn were grouped into two larger macro-units in North/West and South/East of Africa (**Figure 1.5a**). In the North/West savannas, the floristic was partitioned into the Sudanian (drier) and Guinean (wetter) clusters. Within the highly heterogeneous South/East savannas and woodlands, six clusters were identified: Ugandan, Ethiopian, Mozambican, Zambezian, Namibian and South African.

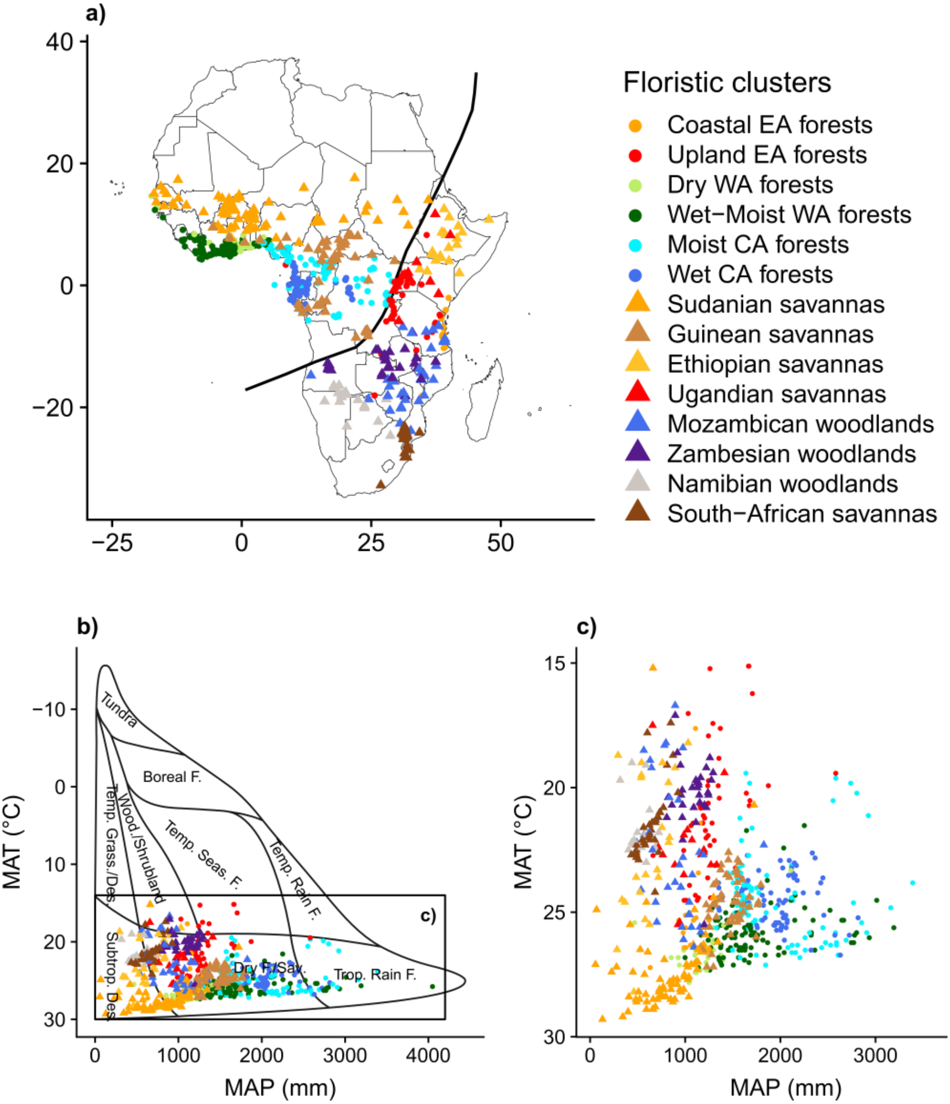

Figure 1.5 Floristic clusters identified by Fayolle *et al.* (2014, 2018) across tropical Africa and plotted in geographical and environmental spaces. The symbols differentiate the clusters assigned to the forest biome (circle) and to the savanna biome (triangle), as originally defined by the authors of the species list collated. (a) Map of the floristic clusters. Each point corresponds to a sample site assigned to a particular floristic cluster. The black line represents the High and Low division of Africa proposed by White (1983), which has been associated with a major floristic discontinuity between the North/West/Central and the South/East part of Africa. (b, c) Environmental space defined by the mean annual precipitation (MAP, in mm) and the mean annual temperature (MAT, in °C) as occupied by sample sites across African forest and savannas an in the original Whittaker plot of biome distribution (b) and in the restricted environmental space occupied by African forest and savannas (c). Adapted from Fayolle *et al.* (2014, 2018).

1.3 The climatic correlates of plant spatial patterns

The association between climate and vegetation are among the earliest ecological observations, dating back to the third century B.C., by Theophrastus in his Enquiry into Plants (Historia Plantarum). At very large scale, climate is implicated as the major driver of vegetation patterning, shaping the structure and the functioning of vegetation. Because of this close relationship, climate-based classification systems have historically been used as proxy for the continental and global biomes patterning (see Box 2016 for a review on the climate-based classifications). For instance, the early works of Köppen (1900) resulted in climatic classification systems that have had a major influence on understanding the global vegetation zonality.

Holdridge (1947) and Whittaker (1970) proposed two simple and consistent bioclimatic systems to infer biome distribution. Holdridge (1947) was the first to create a scheme that positions each biome within an environmental space defined by three climatic axes: temperature, precipitation and potential evapotranspiration. More recently, Whittaker (1970) associated the biome distribution with only two climatic factors: mean annual precipitation and mean annual temperature (**Figure 1.5b**). These two elementary bioclimatic systems are directly relevant to infer the distribution of biomes, even if the inclusion of information on zonal soils conditions (Walter 1973, Walter & Breckle 1985), or on the historical context of the region and disturbance factors can improve predictions. It has been shown that tropical biomes do not necessarily occupy the same environmental space across continents (see Lehmann *et al.* 2014 for savannas, Moncrieff *et al.* 2015 for a global analysis), suggesting a significant influence of history on the vegetation response to climatic drivers. In addition, tropical forests and savannas are not rigidly determined by climate and can be in some places alternative stables states, maintained by disturbance factors such as fire and mega-herbivore grazing (Staver *et al.* 2011).

In tropical Africa, current climate shows clear association with species distribution (Swaine 1996, Bongers *et al.* 1999) and floristic composition (Fayolle *et al.* 2014, 2018). Two main climatic gradients are strongly correlated with the distribution of the floristic clusters defined by Fayolle *et al.* (2014, 2018): precipitation and temperature (**Figure 1.5c**). Across forests, the variation of tree species composition is principally correlated with rainfall. The East African forests (Coastal and Upland) have a drier climate, typically less than 1500 mm/yr and only about 1000 mm/yr along the east coast. Similarly low annual rainfall is found in the dry West African forests, on the margins of the Dahomey Gap. The major floristic discontinuity between the North/West/Central and the South/East parts of Africa is related to a steep change in elevation and temperature. In the South/East part of Africa, the savanna clusters occupied different temperature ranges with relatively low overlap (**Figure 1.5c**). Particularly, the Zambezian cluster occupied higher altitude, cooler and moister sites, whereas the Namibian and South-African clusters occupied drier sites than the other clusters. The Ugandan and Ethiopian clusters both occurred under a wide range of temperatures but were clearly separated along the rainfall gradient.

1.4 The legacy of past climate changes

Climate is the first driver of present-day plant distribution and past climate changes are important drivers of plant migration and extinction, with long-lasting impacts on species diversity and composition (Overpeck *et al.* 1985). Climate fluctuations throughout the Tertiary and Quaternary, as well as tectonic plate movements, have largely determined the dynamics of the distribution of biomes on earth. During much of the last 65 million years, Earth's climate system has experienced continuous change, drifting from extreme of expansive warmth to extremes of cold with massive continental ice-sheets and polar ice caps (Zachos *et al.* 2001; **Figure** 1.5). This long-term climate change has been associated with major shifts in biome distribution, and especially with the long-term range contraction of the tropical forest in Africa (Kissling *et al.* 2012).

Between 55 Ma and 11 Ma ago, the African tropical forest (wet, moist and dry forests) covered from 22 to 15 million km^2. This area dropped to 10 million km^2 3 Ma ago and to 3.4 million km^2 today (Kissling *et al.* 2012). The long-term range contraction of the forest was accompanied by shorter range re-expansion during interglacial periods (Lézine *et al.* 2019; **Figure** 1.7a), especially during the glacial-interglacial cycles of the Quaternary (i.e. 120000 to 12000 years BP). During the cold and arid phases, such as the Last Glacial Maximum (ca. 18000 BP), the wet and moist forests became fragmented while savanna expanded (**Figure 1.7a, b**). During the interglacial periods, forests re-expanded and eventually formed a nearly continuous block. For instance, throughout the Holocene African humid period (ca. 11000–8000 years BP), the forest extended much further of their present range, the Dahomey Gap (a current coastal savanna corridor about 100 km wide separating the Upper and the Lower Guinea Subcentres, as defined by White (1979), **Figure 1.7b**) was forested and the Sahara was crossed by lakes and rivers (Watrin *et al.* 2009, Willis K. J. *et al.* 2013). At the Late Holocene (ca. 3000 years BP) a general degradation of the rain forest is documented in many pollen records from lake or marsh sediments, coinciding with both the onset of a drier climate and the southern expansion of Bantu farmers (Schwartz *et al.* 1996, Ngomanda *et al.* 2009).

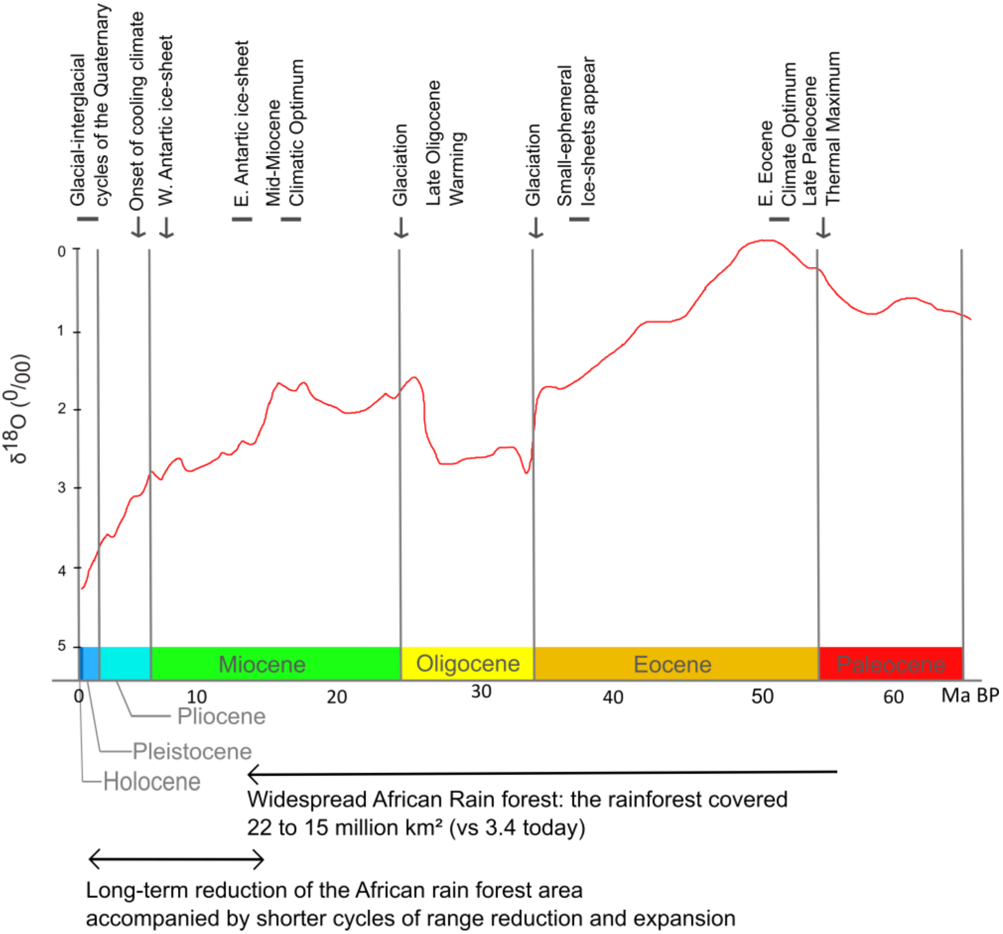

Figure 1.6 Sixty-five Ma to Present global deep-sea oxygen records associated with major climatic events and information of rain forest range reconstruction. During much of the last 65 million years, Earth's climate system has experienced continuous change, drifting from extreme of expansive warmth to extremes of cold. Even if deep water trends are more suitable for high latitude, in the tropics, this long-term climate change has been associated with major shifts in biome distribution, and especially with the long-term range contraction of the tropical forest in Africa (Kissling *et al*. 2012). Adapted from Zachos (2001).

While the current climate is mainly relevant to infer the distribution of floristic assemblage in Africa, the biomes dynamics during these past climate fluctuations have also left an imprint on diversity (Mayr & O'Hara 1986, Maley 1996, Plana 2004, Parmentier *et al*. 2011, Hardy *et al*. 2013, Sosef *et al*. 2017). For instance, across wet and moist forests, high levels of endemism have been detected in several hilly and mountainous regions situated along the Atlantic coast in Lower and Upper Guinea and along the Albertine Rift in the Democratic Republic of Congo (Aubréville 1962, Linder 2001, Tchouto *et al.* 2009). These areas have been proposed as candidate forest refugia during the cold and arid phases of the Pleistocene (*e.g.*, Sosef 1994), acting as 'museums' by remaining climatologically stable through time and accumulating species gradually and experiencing low rates of extinction (Lovett & Friis 1996).

Past climate changes and associated biomes shifts have also been hypothesized as major drivers of diversification (Ackerly 2003, Donoghue & Edwards 2014). Recent data suggests that the forest refugia were not only 'museum' but also acted as major cradles of biodiversity, because the fragmentation of a species range in different refugia favoured allopatric speciation or, at least, genetic differentiation between isolated populations (Hardy *et al.* 2013, Duminil *et al.* 2015). As demonstrated for palm species (Blach-Overgaard *et al.* 2013), the repeated periods of climate warming could have also led to the diversification of several lineages by increasing the opportunity of individuals to adapt to dry and seasonal climates conditions (Donoghue 2008). The extent to which species tracked their native habitat, potentially resulting in species range fragmentation such as recognized for the forest refugia, or adapted as environments have changed is resumed by two crucial evolutionary processes: niche conservatism and niche evolution.

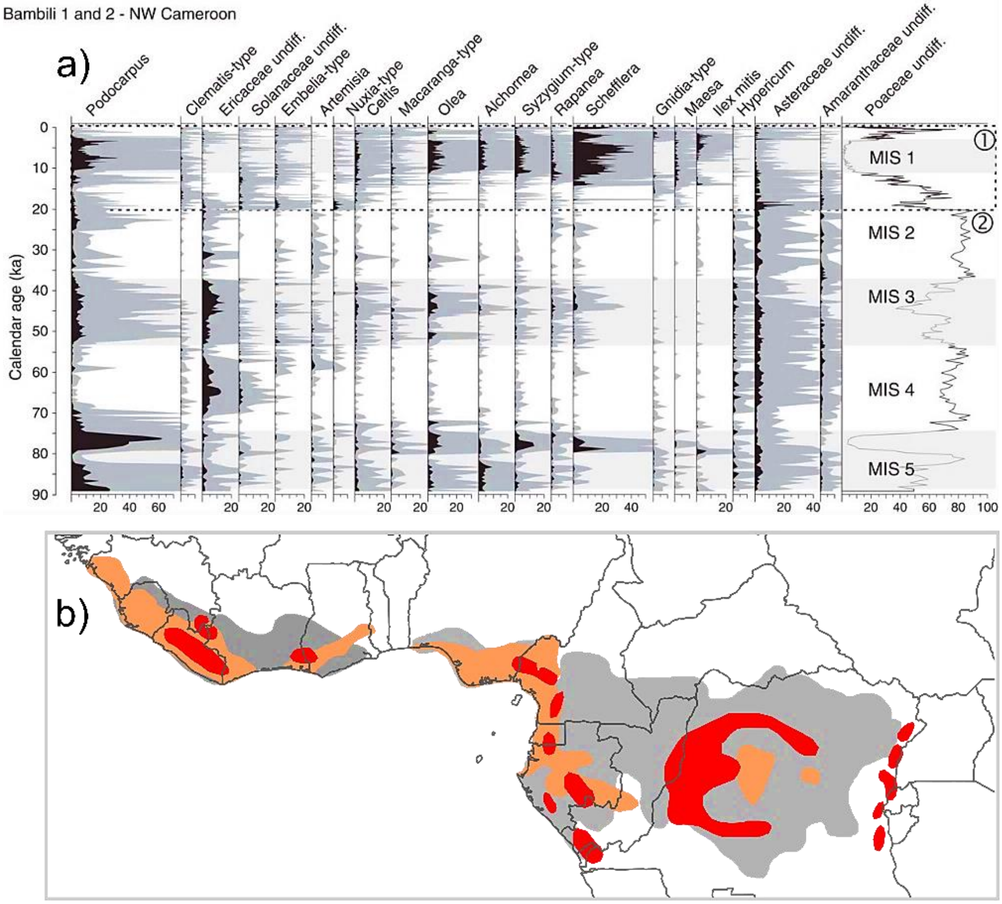

Figure 1.7 Vegetation dynamics during the quaternary glacial periods. (a) Relative frequencies of pollen during the last 90 ka BO at lake Bambili (Cameroon). Black shading indicates selected taxa versus time. Gray shading shows the same results, multiplied by 10 for highlighting. Gray bands indicate the forest phases. Adapted from Lézine *et al.* 2019. (b) Reconstruction of the tropical forest range shifts. Current extent (grey) and hypothetical fragmentation during the quaternary glacial periods according to Maley (1996, in red) and Anhuf (2006, in orange). Adapted from Hardy (2013).

2 The evolutionary processes

2.1 The evolutionary responses to environmental shifts

At species level, niche conservatism and niche evolution over time are two crucial processes explaining biogeographical patterns of plant diversity, distribution and composition (Wiens & Donoghue 2004, Wiens & Graham 2005, Donoghue & Edwards 2014). While the fundamental niche describes all the abiotic conditions in which a species can persist and maintain viable population, the realized niche includes, additionally, constraints arising from interspecific competition (Hutchinson 1978). This set of acceptable conditions is maintained over evolutionary timescale in the case of niche conservatism: the species fail to evolve as the environment changes and instead track their native habitats when the movement is possible. On the contrary, niche evolution, defined as any changes in the niche of a species such as the expansion of the niche breath or the specialization for new conditions, enables a species to disperse into new habitats and climatic regimes, and to persist in changing environment (Wiens & Donoghue 2004, Pearman *et al.* 2008). Niche evolution could result from changing biotic interactions, influencing the realized niche (Pearman *et al.* 2008)[1].

Across phylogeny, the signal of species niche conservatism is called phylogenetic niche conservatism (PNC) and refers to the expectation that related species will tend to occupy similar environments (Donoghue 2008). Phylogenetic studies generally revealed that ecological niches are more conserved through evolutionary history than expected (e.g. Crisp *et al.* 2009, Peterson 2011), implying that adaptations to major climate changes have not been accomplished in all lineages. Many clades in angiosperms are mainly restricted to one of few major biomes. For instance, despite the great variety of environment occupied by the Asteraceae, they are largely more common (higher specific richness) in arid conditions than they are in tropical forest (Donoghue 2008). At global scale, niche conservatism is currently employed to explain the latitudinal gradient in species richness, *i.e.*, the decrease of species richness from equator to the poles. The tropical niche conservatism hypothesis explains the greater richness in tropical regions because most groups originated in the tropics and are specialized for tropical climate (Wiens & Donoghue 2004, Donoghue 2008). Despite millions of years of opportunities, these groups have been unable to disperse into temperate regions because they failed to evolve tolerance to frost. The greater time and area available in the tropics has led to the higher richness for most taxa.

Although it is evident that niche conservatism has played a key role in shaping the distribution of diversity, many lineages have managed to adapt to new environments, resulting in a pattern of phylogenetic niche divergence (PND). For example, while it is true that many of tropical plant lineages have failed to adapt to cold and highly seasonal climate, it is also true that a subset of ancestrally tropical plant lineages have succeeded in making this transition, such as the the woody angiosperm clade *Viburnum* (Adoxaceae, Schmerler *et al.* 2012). Simple evidences of niche evolution

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[1] According to Pearman *et al.* (2008), studies on niche evolution should, first, be based on the quantification of the fundamental niches and, second, be constrained by the effects of biotic interactions. Given that the fundamental niches can only be estimated using costly manipulative experiments in the field and/or under controlled conditions, these estimates have only been conducted for a few species. In the absence of data from manipulative experiments, niches are often modelled with field observation data and included effects of biotic interactions and, therefore, correspond to realized niches.

are also provided because there are ecologically distinctive clades within several families (such as the hyperdiverse Fabaceae and Bignoniaceae families) or because through the most recently biomes are occupied (Donoghue & Edwards 2014). Niche evolution obviously occurs, and may even be the norm under certain circumstances, such as climate changes.

2.2 The move or evolve dilemma

Through environmental changes, such as climate warming, the extent to which the niche of a species is conserved or evolved is function of two key variables: the rate of dispersal and the rate of trait evolution. This principle can be summarized by the sentence: '*it is easier to move than to evolve, unless it isn't*' (Donoghue 2008).

In a case of niche conservatism, the species fail to evolve *in situ* as the environment changes and instead track their native habitats when the movement is possible (species A in **Figure 1.8**). This scenario is achievable if suitable corridors exist for the dispersion of species and allow them to move into the appropriate regions relatively quickly. The incapacity of some species to adapt to changing conditions combined with limitation in dispersal has probably driven extensive extinctions during dramatic climatic events (species D in **Figure 1.8**) or led to the contraction and/or the fragmentation of the geographical range of species, as was the case for several African lineages restricted into forest refugia during past climatic events of the Pleistocene. In this case, niche conservatism is expected to be an important and widespread component of allopatric speciation (Wiens 2004). Under the same environment, genetic processes such as genetic drift[2] or uniform selection[3] can lead to non-ecological speciation between allopatric populations (Rundell & Price 2009, Sobel *et al.* 2010), resulting in PNC.

In the other hand, long-term shifts in climate and the exposure of the population to new environments also increase the adaptive evolution opportunities (Donoghue & Edwards 2014). In a case of niche evolution, the species could adapt to the new conditions (niche evolution, species C-C' in **Figure 1.8**). The species could also migrate *and* evolve (species B and B' in **Figure 1.8**), which potentially result in ecological speciation[4] when the selection leads to reproductive isolation between populations (Rundell & Price 2009, Nosil 2012). That's why, the repeated past climate

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[2] reproductive isolation between allopatric populations due to alternate mutations fixed by stochastic processes (random changes in the frequency of alleles in a gene pool).

[3] allopatric populations experience the same selective environment and evolve by fixing different adaptive mutations, resulting in similar phenotypes but reproductive isolation.

[4] the process by which barriers to gene flow evolve between populations as a result of ecologically based divergent selection between environments. Divergent selection could operate directly on reproductive traits or because traits under divergent selection, or those correlated with them, incidentally effect reproductive selection.

warming during Quaternary have been hypothesized to be major drivers of evolutionary shifts between the forest and savanna biomes.

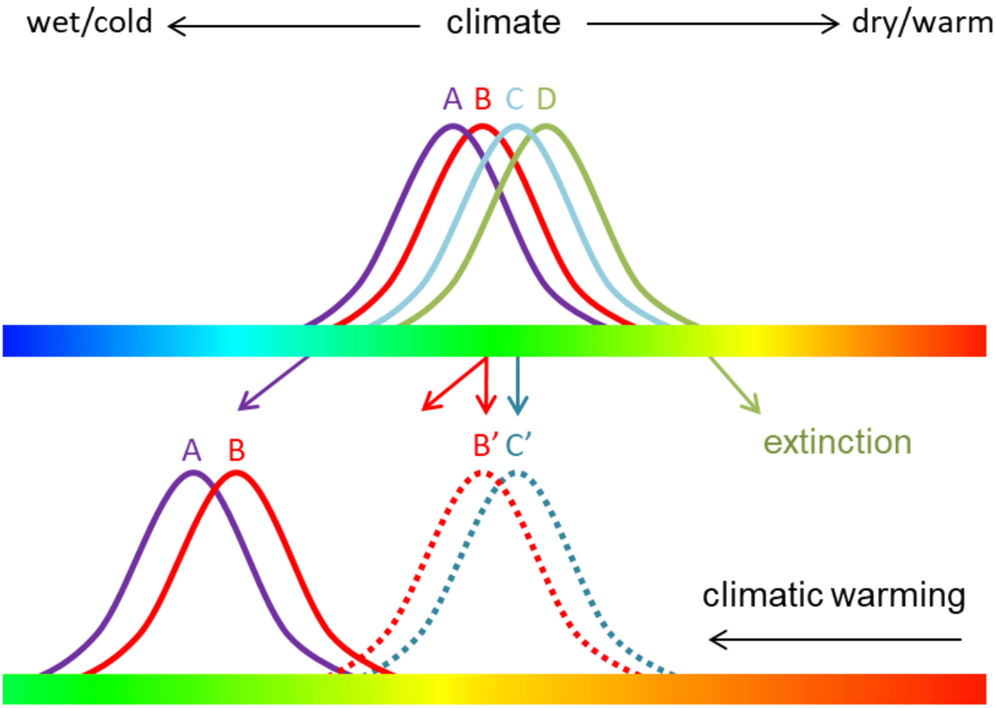

Figure 1.8 Hypothesized responses of species to climate change. In a case of niche conservatism, the species migrate and track their native habitat, (species A) or go extinct (species D). In a case of niche evolution, species adapt to the new condition (species C-C') or might migrate and evolve in situ, potentially resulting in ecological speciation (species B-B'). Figure adapted from Ackerly (2003) and Donoghue & Edwards (2014).

Of course, these scenarios are simplistic and the current pattern of phylogeny certainly results from multiple processes, which probably lie in between the cases mentioned above. For instance, adaptive differentiation can occur after a non-ecological speciation between isolated populations (Rundell & Price 2009). Otherwise, ecological speciation between populations previously isolated may be common because allopatric populations will often occur in environments with subtle differences and experience absence or very low gene flow between them ("habitat isolation"; Rundle & Nosil, 2005).

2.3 The evolution of traits within lineages

The probability that a lineage will successfully diversify into a novel habitat depends on the exposure to this new habitat and also to the likelihood of realizing different ecologically adaptive phenotypes (*i.e.*, traits evolution). This second factor is expected to vary enormously from lineage to lineage, with lineages possessing “enabler traits” (*sensu* Donoghue 2008), predisposing them to make certain ecological transitions. One of the few recognized examples of major ecological evolution is that of the appearance of C_4 photosynthesis in grass clades ancestrally originated from tropical forest understory. Despite the complexity of this adaptation, this ecological evolution has been detected 26 times within the last 10 million years, mostly within a unique clade (Edwards & Smith 2010). Aside from this remarkable case of trait evolution, little is known about the morphological and physiological shifts that allow a particular lineage to disperse in contrasting environments.

2.4 The biome shifts within tropical tree lineages in Africa

As mentioned above, PNC has been identified for many lineages (e.g. Crisp *et al.* 2009, Peterson 2011) and, comparatively, few niche evolutions have been reported in phylogenetic studies (see Donoghue & Edwards 2014 for a review on biome shifts). In Africa, while some genera have been associated with specific biomes (Linder 2014), evidence of widely distributed genera transcending biome or habitat boundaries have also been reported for herbaceous plants (for palms species see Blach-Overgaard *et al.* 2010, or for the *Coccinia* genus Holstein & Renner 2011) and for trees (see the early work of White 1978 on *Diospyros,* and the more recent genetics studies of Donkpegan 2017 on *Afzelia*, and Tosso 2018 on *Guibourtia*). Using the RAINBIO dataset, we identified more than 190 tropical tree genera encompassing both forest and savanna species (**Figure 1.9**). The evolutionary processes that allowed these particular lineages to disperse and adapt into new environments, transcending biomes boundaries, are far from being resolved. Therefore, within these lineages, dissecting the strategies of the species and understanding the functional traits involved in those strategies could be the strongest evidence for niche evolution and will allow the understanding of the mechanistic underpinnings of ecological transitions (Westoby 1998, Wiens & Donoghue 2004).

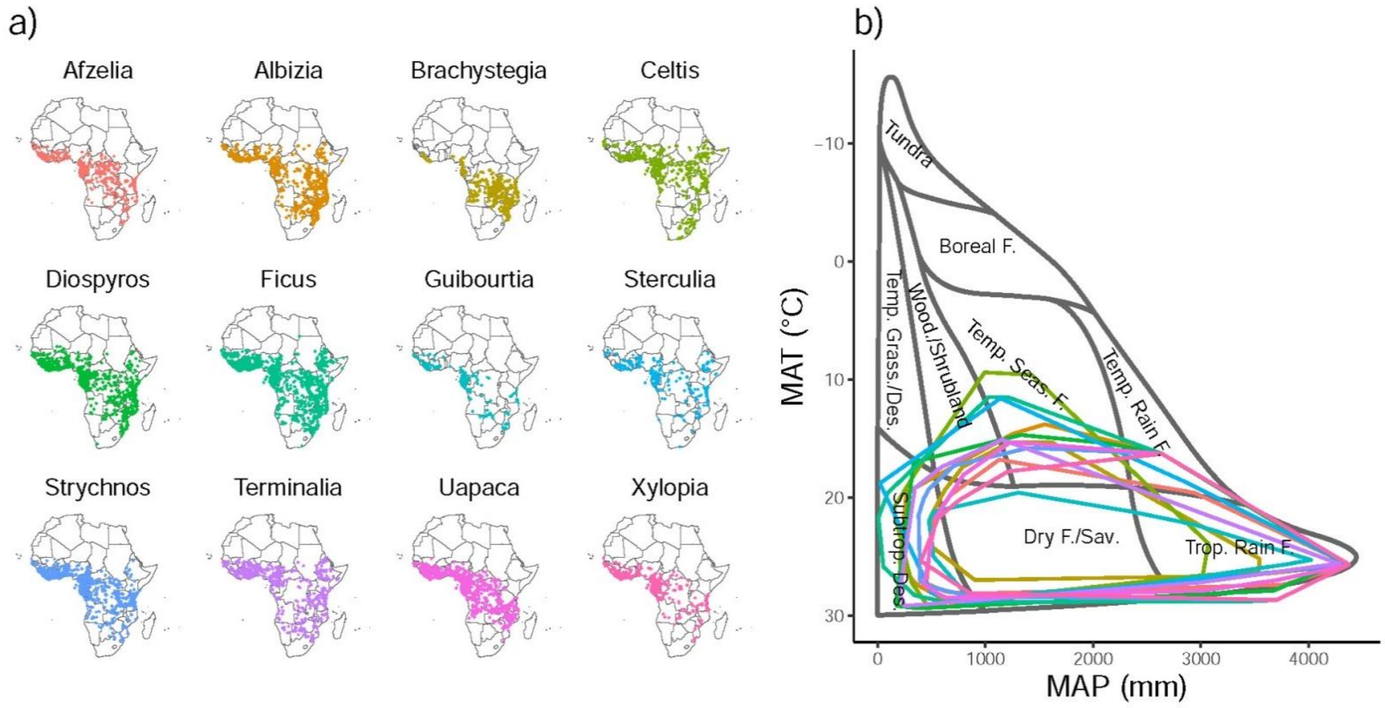

Figure 1.9 Distribution in geographical space and in Whittaker‘s bioclimatic scheme for 12 African tree genera transcending forest and savanna boundary. Data are extracted from the RAINBIO dataset, available at http://rainbio.cesab.org/.

3 The functional understanding of tropical tree diversification

3.1 The functional trait approach

The niche, strategy and trait concepts are widely used in evolutionary biology and in plant ecology, with not necessarily the exact same meaning. In plant ecology 'strategy' is defined as 'how a species sustains a population in the presence of competing species, in varied landscapes and under regimes of disturbance' (Westoby 1998, Reich 2014). The strategy of a plant species is underpinned by trade-offs in resource use: the allocation of limited resources to one purpose *vs* another. One fundamental axis of evolutionary specialization across ecosystems is that of rapid acquisition of resources at one end of the spectrum and conservative use of resources at the other end (Diaz *et al.* 2004, Wright *et al.* 2004, 2010). Plants at the 'fast' end of the acquisition-conservation trade-off had high growth potential when resources are available. In contrast, plants at the 'slow' end of the trade-off survived better when the resources are scarce. To explain the position of a species on this slow-fast continuum, the role of multiple variations in morpho-physio-phenological plant traits (*i.e.,* the 'functional traits' sensu Violle *et al.* 2007) have been reported for leaves (the leaf economic spectrum, Wright *et al.* 2004), stem (the stem economic spectrum, Chave *et al.* 2009) and roots (Bardgett *et al.* 2014), each viewed independently. Reich (2014) demonstrated the link across organs and coupling among resources, resulting in an integrated whole-plant economics spectrum. Species capable of moving water rapidly have low tissue density, short tissue life span and high rates of resource acquisition and flux at organ and individual scales.

3.2 The drought strategies of tropical trees

The biome shift from forests to drier habitats relies on niche evolution along rainfall and temperature gradients. This suggests adaptation to drought and the adoption of a conservative water use strategy could be important for the success of the plant species. For trees, conservative water use can be achieved through efficient use of limited water (i.e. desiccation tolerance) or through desiccation avoidance (Tyree *et al.* 2003, Markesteijn & Poorter 2009). The desiccation tolerance strategy is promoted by physiological traits that sustain continued water transport, gas exchange, or cell survival at low water content (WC) and low water potential (Ψ), such as resistance of xylem to embolism, and the ability of cells to remain alive at low WC and Ψ. In contrast, the desiccation delay strategy involves traits that increase access to water and reduce water loss, including deep roots, early stomatal closure, water storage in plant organs, photosynthetic stems and leaf shedding (Westoby *et al.* 2002, Lachenbruch *et al.* 2011, Santiago *et al.* 2016).

In the tropics, the paucity of data on drought resistance strategies, and especially on hydraulics traits has to be noted (see Choat *et al.* 2007 for available hydraulic data), specifically for African tree species (but see Epila, Maes, *et al.* 2017 for *Maesopsis eminii* (Malvaceae)).

3.3 The wood hydraulics and associated anatomical traits

Sensitivity of xylem to embolism represents an important constraint on tree functioning and survival during drought (Brodribb & Cochard 2009, Urli *et al.* 2013, O'Brien *et al.* 2017). Intense drought reduces plant water potential, leading to the embolism of the xylem water column, the cessation of water supply to leaves and finally plant death (i.e. the hydraulic failure, McDowell *et al.* 2008). Quantifying the resistance of a plant to embolism, by measuring the relationship between xylem pressure and loss of hydraulic conductivity due to conduit occlusion by gas emboli, has been the principal approach to characterize drought resistance in woody species (Choat *et al.* 2007, 2012, Santiago *et al.* 2016; **Figure** 1.11a). $\Psi_{50,}$ the water potential at which the xylem experiences 50 % loss of conductivity is the most commonly used index of embolism resistance (**Figure 1.10**). Low embolism resistance is associated with high transport efficiency and low structural 'costs', making this an advantageous acquisitive strategy in highly productive environments (Sperry *et al.* 2008, Choat *et al.* 2012). In a recent publication, Körner (2019) affirmed that xylem embolism is a byproduct of the disruption of the soil-root capillary continuum, the latter being the main cause of tree death under severe drought. However, the association between critical degree of tree dehydration and the vulnerability of the xylem to embolism is not called into question and the action of evolutionary selection on this traits is emphasized.

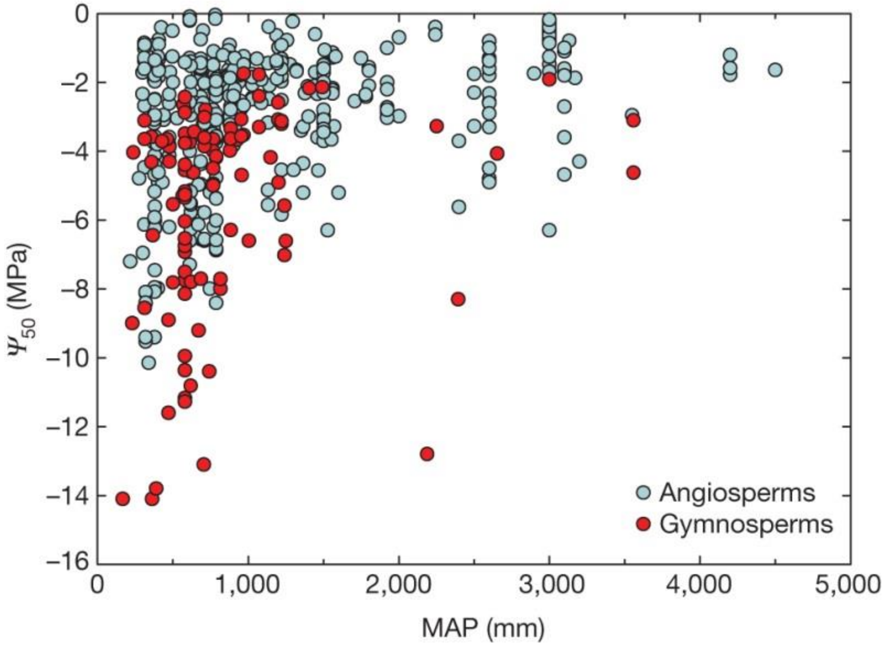

Figure 1.10 Embolism resistance (Ψ_{50}) plotted against mean annual precipitation (MAP) for 384 angiosperm and 96 gymnosperm species across the world. Ψ_{50} is the water potential at which 50% loss of conductivity occurs. Ψ_{50} is the most commonly used index of embolism resistance. Each point represents one species. Extracted from Choat *et al.* (2012)

More recently, the used of stored water to supply the transpiration stream and protect xylem from precipitous drops in water potential has emerged as one of the most important aspects of tree hydraulics (Scholz *et al.* 2011, Vergeynst, Sause, *et al.* 2015, Epila, Maes, *et al.* 2017). Tropical trees with high capacitance have been shown to survive drought even with low embolism resistance, because of the buffering role of stored water and the lower risk of reaching the xylem tension that causes hydraulic failure (Meinzer *et al.* 2004, Sperry *et al.* 2008, Epila, Maes, *et al.* 2017, Wolfe 2017). The hydraulic capacitance, defined as the amount of water released from the tissue into the xylem per unit decrease in ψ, is calculated for two distinct phases as the slope of the linear regression between the wood volumetric water content and the water potential Ψ (*i.e.* the desorption curve; Vergeynst, Dierick, *et al.* 2015). The elastic phase or phase I (**Figure 1.11b**), and the related capacitance, occurs when water is released from the elastic shrinkage of living cells. In contrast, the inelastic phase or phase II (**Figure 1.11b**) occurs when embolism is strong and water is released from embolized conduits into the still functional ones (Vergeynst, Dierick, *et al.* 2015, Epila, Baerdemaeker, *et al.* 2017). In addition to the above-mentioned water flows, a greater focus on the dynamics of the internals water pools may improve the capacity to monitor and anticipate drought-induced mortality (Martinez-Vilalta *et al.* 2019).

Wood anatomy indeed directly relates to conductivity, xylem safety and hydraulic capacitance (Borchert & Pockman 2005, Lachenbruch & McCulloh 2014, Beeckman 2016). Angiosperms with wide vessels have higher water transport efficiency, but are more vulnerable to embolism (Zanne *et al.* 2014, Gleason *et al.* 2016). However, vessel size and abundance only partially explain conductivity and xylem safety (Choat *et al.* 2008). The passage of sap flow through the intervessel pits, the vessel cell-wall reinforcement and the connectivity of the conduit network are at least as important as conduit size and abundance. In addition, the high water storage capacity of parenchyma of the secondary xylem is expected to contribute to hydraulic capacitance together with the conduits (Anderegg & Meinzer 2015, Morris & Jansen 2016, Epila, Maes, *et al.* 2017).

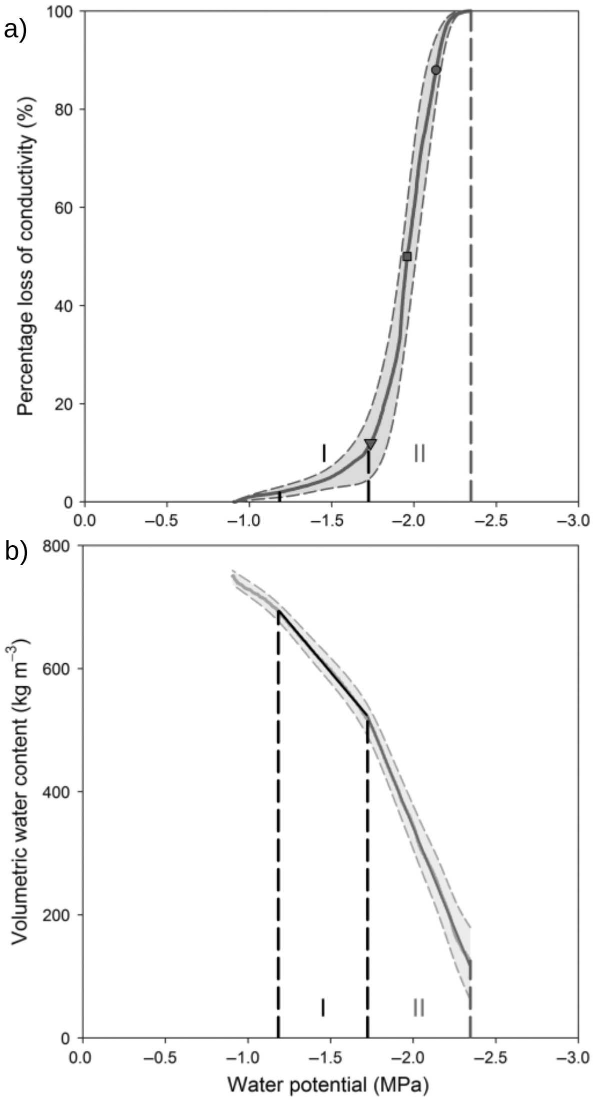

Figure 1.11 Average vulnerability curve (a) and desorption curve (b) of *Maesopsis eminii*, an African forest tree species. Average vulnerability curve was obtained by plotting the percentage loss of conductivity against xylem water potential during the bench dehydration experiment. The vulnerability thresholds ψ_{12} (triangle), ψ_{50} (square), ψ_{88} (circle) and ψ_{100} (dashed line) are indicated as well. The desorption curve was obtained by plotting the volumetric wood water content against xylem water potential. Phases I and II are delimited by vertical lines and the slopes within these phases represent elastic and inelastic hydraulic capacitance, respectively. Extracted from Epila, Baerdemaeker, *et al.* (2017).

3.4 The regulation of gas exchanges

In addition to hydraulic capacitance, the regulation of gas exchanges could buffer xylem from reaching critical water potential and prolong survival during drought (Pivovaroff *et al.* 2016). When the supply of water decrease, plants could close their stomata to reduce transpiration rates and maintain the integrity of the water transport pathway (Sperry 2003). The terms isohydric and anisohydric have been used to describe the opposite ends of a broad continuum of water-use strategies (McDowell *et al.* 2008). On the one hand, isohydric plants close their stomata early in response to drought, thereby maintaining high leaf water potential and avoiding hydraulic failure due to xylem embolism. On the other hand, anisohydric species exhibit lower stomatal responsiveness and maintain high transpiration rates and high productivity. It is now apparent that perfect iso- and anisohydric behavior is rare if it exists at all (Martínez-Vilalta *et al.* 2014). Though, iso/anisohydry is a useful concept, the way plants regulate their water status as measured by water potential is highly complex (Ratzmann *et al.* 2019).

3.5 The stem photosynthesis

Chlorophyll in stem tissues might play a crucial role in the drought-resistance of trees (Vandegehuchte *et al.* 2015). During drought, trees can minimize the risk of hydraulic failure by closing their stomata or by leaf shedding, however, these drought-avoidance strategies limit CO_2 uptake. In this case, stem photosynthesis is expected to provide a large proportion of total carbon. Woody tissue photosynthesis may even result in a positive net photosynthetic rate in some species because of the combination of internal recycling of CO_2 and additional fixation of atmospheric CO_2 directly transported to the stem chlorenchyma through lenticels (Ávila-Lovera *et al.* 2017). Moreover, as demonstrated for poplar, stem photosynthesis could be important for maintaining the hydraulic function of the vasculature by fulfilling local energetic and carbohydrate demands for maintaining cell turgor (Bloemen *et al.* 2016) and by decreasing xylem vulnerability to embolism via sugar-mediated mechanisms (De Baerdemaeker *et al.* 2017).

4 Our research strategy

4.1 Approach and objectives

In this thesis, I aimed to understand the evolutionary processes that allowed particular lineages to occupy vast areas, transcending habitats and biomes boundaries. While a diversity of methods at different phylogenetic and spatial scales can provide complementary insights, detailed analyses of resolved clades are needed to build robust generalizations (Donoghue & Edwards 2014). The comparison of ecological strategies and underlying traits between species and populations within a genus provides a direct measure of the evolutionary divergence relative to a common ancestor (Ackerly 2003) and provide a functional understanding of diversification.

From species distribution modeling to sharp physiological measurements, I attempted to disentangle the processes behind the large-scale distribution of the *Erythrophleum* genus, which transcended significant ecological boundaries, resulting in biome shift from forest to savanna, as reported for other congeneric species (**Figure 1.9**). In tropical regions and specifically in Africa, the paucity of research on biogeography and diversification is mainly due to the scarcity of well-resolved taxonomic identification and of the associated ecological and distributional data (Beheregaray *et al.* 2015). That's why, *Erythrophleum* (Fabaceae - Caesalpinioideae), much investigated for genetics in Central Africa (Duminil *et al.* 2011, 2015) is a providential model to study how trees adapt and colonize wide environmental ranges (Gorel *et al.* 2015).

4.2 Structure of the thesis

In the **Chapter 2,** we summarized the current knowledge on the African species of *Erythrophleum,* specifically the knowledge relative to the phylogeography. As mention above, the geographical delineation of populations and species with clear insights on genetics is fundamental to generate conclusion about diversification processes (Beheregaray *et al.* 2015). A state-of-the-art on the *Erythrophleum* genus was published in French in a paper entitled "Ecology and management of the multipurpose *Erythrophleum* species (Fabaceae-Caesalpinioideae) in Africa. A review" (Gorel *et al.* 2015) and transcribed in this document in this chapter.

In the **Chapter 3**, we used species distribution models to determine the bioclimatic constraints on the distribution of the *Erythrophleum* species across tropical Africa, and of *Erythrophleum ivorense* and *Erythrophleum suaveolen*s gene pools in the Upper and Lower Guinean Subcentres. Then, we combined the available phylogenetic data with information on ecological niche divergence to explore the diversification history. We specifically tested whether the adaptation to specific climatic conditions played a role in the distribution and diversification within the genus. The adaptation in response to climate has been expected to result in species/pools pairs adapted to different habitats and presenting clear climatic niche divergence. This study has been published in *Plant Ecology and Evolution* in a paper entitled "Ecological niche divergence associated with species and populations differentiation in *Erythrophleum* (Fabaceae - Caesalpinioideae)" (Gorel, Duminil, *et al.* 2019).

In the **Chapter 4**, we conducted *in situ* measurements to precisely explore how related tree species could evolve on an aridity gradient. Using an integrated eco-physio-morphological approach, we compared the two sister species, *E. ivorense* and *E. suaveolen*s, which occupy contrasting forest types and rainfall conditions in Upper and Lower Guinea. We examined between-species variation in hydraulics including vulnerability to embolism, wood water content and capacitance, and we determined the underlying wood traits, especially the vessels-associated traits. Growth and life-history traits were also examined. A common garden was specifically used to test whether differences in growth and wood traits are maintained under the same environment. This study has been published in *Biotropica* in a paper entitled "Testing the divergent adaptation of two congeneric tree species on a rainfall gradient using eco-physio-morphological traits" (Gorel *et al.* 2019).

In the **Chapter 5,** we used a controlled experiment to examine the effects of drought on the physiology, wilting and mortality of 1-year old seedlings of the two sister species: *E. ivorense* and *E. suaveolens*. In order to locate the two species along the continuum of iso- to anisohydric behavior, we measured leaf gas exchanges and plant water status of control (well-watered) and drought-stressed (water-withheld) seedlings over time. To examine the contribution of woody tissue photosynthesis to drought-tolerance, half of the drought-stressed seedlings were subjected to a stem light-exclusion treatment to prevent bark and woody tissue photosynthesis.

Since the concepts presented in the introduction sections of the published papers have been combined and strengthened in this general introduction (**Chapter 1**), the methods, results and discussions are solely detailed in the **Chapters 2-5**. Nevertheless, the aims and hypotheses tested are given in preambles, so that the connections between chapters are clear.

Finally, in the **Chapter 6**, I summarized the major results of this work and confronted them with other studies on congeneric species. Then, I discussed the generalization of the niche evolution pattern I detected for *Erythrophleum* to other African genera by providing preliminary results of a continental analysis based on the niche comparison of 1439 woody species belonging to 532 genera (Gorel & Fayolle, in prep). Finally, I concluded with the practical implications of this work.

2

Study species

1 Preamble

In tropical regions and specifically in tropical Africa, the paucity of research on biogeography and diversification is mostly due to the scarcity of taxonomic, ecological and distributional data. The geographical delineation (*i.e.* with clear insights from genetic data) of populations and species is fundamental to generate conclusions about diversification processes (Beheregaray *et al.* 2015). The next chapter proves that *Erythrophleum* in Africa offers a very good model for the study of the diversification processes of tropical tree lineages, because this genus occupies vast area in Africa, and its phylogeography is largely resolved and described by genetics.

Erythrophleum is a pan-tropical tree genus represented by seven species worldwide. Four parapatric species occur in tropical Africa: *Erythrophleum ivorense* A.Chev, *Erythrophleum suaveolens* (Guill. & Perr.) Brenan, *Erythrophleum africanum* Harms and *Erythrophleum lasianthum* Corbishley. One species is endemic to Madagascar (*E. couminga* Baill.), one occurs in Australia (*E. chlorostachys* (F.Muell.) Baillon) and one in China (*E. fordii* Oliver). Based on an extensive literature review, we summarized in this chapter the available information on the African *Erythrophleum* species in terms of botany, phylogeography and ecology.

The complete state-of-the-art on the *Erythrophleum* genus was published in French: Gorel, A-P., Fayolle A., and Doucet J.-L. 2015 *Écologie et gestion des espèces multi-usages du genre* Erythrophleum *(Fabaceae-Caesalpinioideae) en Afrique (synthèse bibliographique).* Biotechnol Agron Soc Env. 415–429.

2 Botanical insight

All the individuals belonging to the *Erythrophleum* genus are unarmed trees with alternate and bipinnate leaves. The stipules are very small and fall quickly. A gland is located at the base of each pair of pinnae on the main rachis. The inflorescence is a panicle composed by pedunculate spike-like racemes. The bracts are very small and fall before or during the opening of the flowers. The flowers are hermaphroditic, have a bell-shaped calyx with five fused or almost free lobes. The five petals are free and equal, imbricated, more or less pubescent or tomentose. The ten stamens are often alternately long and short and the filaments are glabrous or hairy. The ovary is tomentose or densely pubescent, containing several ovules. The stigmas are punctiform, cup-shaped and minutely ciliolate. The pods are oblong or oblong-elliptic, woody or tough, dehiscent and contain 2 to 11 seeds. The seeds are attached by a long funicle, not areolate, have an endosperm and are arranged transversely in the pod (Aubréville 1959, Brenan 1967, Hawthorne 1995).

Figure 2.1 Crown (a), trunk and bark (b), pods (c), leaves and flowers (d), and flowers (e) of *Erythrophleum suaveolens.* Photos J-L Doucet, A. Gorel

The African *Erythrophleum* species are morphological similar and very hard to distinguish in the field. In order to facilitate the identification, a synthesis of the botanical knowledge is presented as an identification key based on chorological, vegetative and reproductive characteristics[5]:

1. a. African species of dense forests or gallery forests; stamen with glabrous filaments; initial dehiscence of the pod on a single suture….. 2

   b. African species of woodlands and savannas; stamen with pubescent or tomentose filaments; dehiscence of the pod simultaneously along both sutures…………………………………… 3

2. a. Leaflets 8.5×4 cm, cuneate to subrounded at the base; leaf blade glabrous, brownish and shiny when dry; flowers around 3 mm, reddish-brown, sub-sessile with a 0.5 mm peduncle; petals densely hairy outside, smooth inside; circular bracts, more or less persistent; pods 3.5-4×7-8 cm; 2 to 10 seeds 13-15×9-10×4-7 mm; coastal wet forest of the Guineo-Congolian Centre of endemism…………………………………………………………… *E. ivorense*

   b. Leaflets up to 9×5.5 cm, subrounded and asymmetric at the base; leaf blade with midrib usually pubescent, greenish and matt when dry; flowers up to 7 mm; greenish-white, pedunculate (often 1.5 mm); petals pubescent outside, sometimes only at the edges and on the midrib; without bract; large pods of 5-7×14-15 cm; 5 to 11 seeds 16-19×10-12×4-7 mm; moist and dry forests in the Guineo-Congolian Centre of endemism; dry forest and gallery forest in the Transition zones around the Guineo-Congolian Center of endemism and restricted to patches of dry forest in the Zambezian Centre of endemism…………………… *E. suaveolens*

3. a. Rachis, petiole and petiolules pubescent or tomentose; leaflets up to 6.5×3.5 cm, not acuminate; leaf blade usually pubescent above and below, with conspicuous secondary ribs; flowers up to 4 mm, yellowish-white to reddish; calyx-lobes almost free; pods 2.2-4.5×7-19 cm, with median stipe; 2 to 5 seeds 10-14×8-12×3-4 mm, with thin endosperm; woodland and savanna in the Sudanian and the Zambezian Centres of endemism and in the Transition zones around the Guineo-Congolian Center of endemism ……………………........ *E. africanum*

   b. Rachis, petiole and petiolules glabrous; leaflets up to 5×3.5 cm, acuminate; leaf blade glabrous, with inconspicuous secondary ribs; flowers up to 7-11 mm, greenish-yellow to cream; calix-lobes distinctly fused from one-third to half; pods 3-4×7-16 cm, with lateral stipe; 5 to 11 seeds 12-15×10-13×4-6 mm, with thick endosperm; woodland north of the Tongaland-Pondoland Regional mosaic..…………………………………………………… *E. lasianthum*

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[5] Based on Aubréville 1959, 1968, 1970, Brenan 1967, Moll 1977, Vivien & Faure 1985, Pooley 1993, Hawthorne 1995, Wyk & Wyk 1997, Poorter 2004, Akoègninou *et al.* 2006, Arbonnier 2009

3 Geographical distribution and habitats

The *Erythrophleum* genus is widely distributed in Africa. The species and the gene pools within *E. ivorense* and *E. suaveolens* occur in adjacent geographical and climatic areas (**Figure 2.2**).

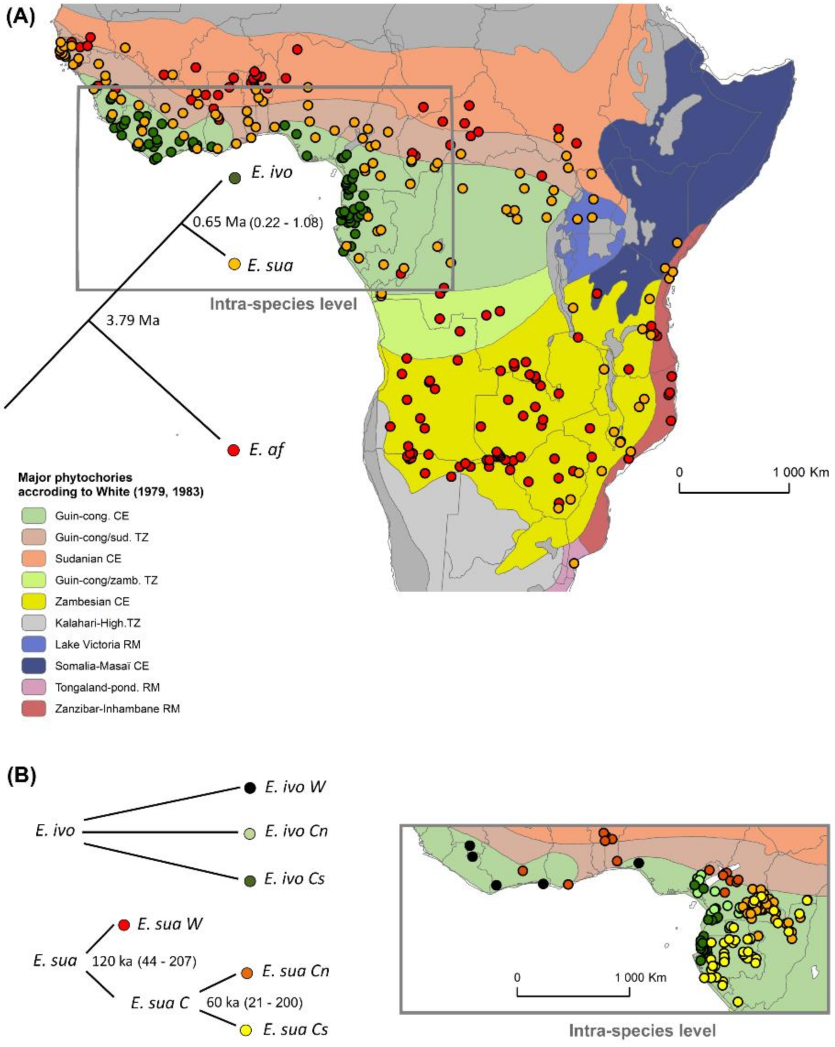

Figure 2.2 Schematic cladograms and distribution of tropical African *Erythrophleum* species (a) and gene pools (b). Occurrence data overlaid on a base map showing the boundaries of the major phytochoria according to White (1983; Mollweide projection) with abbreviations corresponding to Centre of Endemism (CE), Regional Mosaic (RM) and Transition Zone (TZ). Mean dates of divergence (and, if available, the 95% highest posterior density interval in parentheses) according to Duminil *et al.* (2015) are indicated on the cladograms.

Erythrophleum ivorense is restricted to the coastal wet forest of the Guineo-Congolian Centre of endemism (White 1983), with a disjunct distribution, being absent from the arid Dahomey Gap (Duminil, Heuertz, Doucet, *et al.* 2010), a coastal savanna corridor about 100 km wide separating the Upper and the Lower Guinea Subcentres .

Erythrophleum suaveolens is widespread across tropical Africa, being distributed from the Guineo-Congolian/Sudanian Transition zone, through the entire Guineo-Congolian Centre, with the notable exception of the wet forest areas that are occupied by *E. ivorense,* to the Zambezian Centre of endemism and the Zanzibar-Inhambane Regional mosaic. In the Guineo-Congolian Centre, *E. suaveolens* occurs in the moist and dry forests (Duminil, Heuertz, Doucet, *et al.* 2010). In more arid areas, such as the Guineo-Congolian/Sudanian transition zone, *E. suaveolens* is restricted to the dry forest along the coast in the Dahomey gap, or to gallery forest inland (De Wolf 1998, Goetze *et al.* 2006, Chidumayo & Gumbo 2010). In the Zambezian Centre of endemism, *E. suaveolens* appears to be restricted to patches of dry forest scattered within the woodlands (Lawton 1978, Tuite & Gardiner 1990).

Erythrophleum africanum is broadly present in the Zambezian and Sudanian Centres of endemism and in the Transition Zones around the Guineo-Congolian Centre. While *E. suaveolens* is limited to patches of dry forest in these regions, *E. africanum* largely occurs in the woodland and the pyrophytic savanna (Wyk 1996, Wyk & Wyk 1997).

Erythrophleum lasianthum is restricted to the Tongaland-Pondoland Regional mosaic. The species is typical of the dry and riparian forests on sandy soils where the species dominates with *Dialium schlechteri* (Moll 1977, Wyk 1996, Wyk & Wyk 1997).

4 Phylogeography

Erythrophleum ivorense and *E. suaveolens* are genetically closer to each other than *E. africanum*. The mean date of speciation between *E. ivorense* and *E. suaveolens* was estimated at 0.65 Ma (compared to 3.79 Ma between *E. africanum* and the common ancestor of *E. ivorense* and *E. suaveolens*, Duminil *et al.* 2015, **Figure 2.2**). No speciation date has been yet calculated for *E. lasianthum*.

In the Upper and Lower Guinean Subcentres, a strong spatial genetic structure, mainly parapatric, has been identified within both *E. ivorense* and *E. suaveolen*s (Duminil *et al.* 2013, **Figure 2.2b**). Duminil *et al.* (2013) identified three gene pools within *E. ivorense* and three gene pools within *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 the Central Africa (*E. ivo Cn* and *E. sua Cn*) and in the southern part of the Central Africa (*E. ivo Cs* and *E. sua Cs*, respectively, **Figure 2.2b**).

Between *E. suaveolens* and *E. ivorense* and between the gene pools within *E. suaveolens*, the divergence dates are concomitant with the Pleistocene climatic cycles (Duminil *et al.* 2015), arguing for a role of past climate changes into diversification. The climate-driven contractions of lowland forests during glacial periods, especially during the last glacial episode of the Pleistocene (i.e. 120000 to 12000 years BP), have probably boosted the speciation between *E. suaveolens* and *E. ivorense* and the genetic differentiation within *E. suaveolens* (Maley 1996, Hardy *et al.* 2013, Duminil *et al.* 2015).

5 Ecological insight

The ecological data on the *Erythrophleum* species are still sparse and more complete for *E. ivorense* and *E. suaveolens*, which are widely used for timber.

5.1 Light requirement and population structure

Erythrophleum ivorense and *E. suaveolens* are non-pioneer light demander species (Hawthorne 1995, Doucet 2003). A lack of young stems has been detected in populations in Cameroon, Gabon and North Congo, reflecting the poor natural regeneration of these species (Durrieu de Madron *et al.* 2000, Doucet 2003, Kouadio 2009). *Erythrophleum africanum* is a pyrophyte pioneer species which only establishes in open environments, often after the passage of fires (Lawton 1978). No published data on the light requirement of *E. lasianthum* and the population structure of *E. africanum* and *E. lasianthum* is available to our knowledge.

5.2 Phenology

The phenology of the African *Erythrophleum* species is relatively regular, annual and seasonal (Childes 1988, Hawthorne 1995, Richer 2008, Arbonnier 2009, Kouadio 2009). A phenological time-lag has been detected between species, and also between populations of the same species, south and north of the climate hinge **(Table 2.1**), reflecting potentially the seasonal shift between the northern and the southern climates (Suchel 1990, Gonmadje *et al.* 2012).

Erythrophleum ivorense, *E. suaveolens* and *E. africanum* are deciduous species. Leaf fall is not synchronous between individuals, occurring gradually from one tree to another and from one branch to another on the same tree (Childes 1988, Richer 2008, Kouadio 2009). The flowering is associated with rainfall. North of the climatic hinge, *E. ivorense* flowers between (May-) June and September (-October), which corresponds to the middle of the wet season (Aubréville 1959, Voorhoeve 1965, Poorter 2004). The flowering of *E. suaveolens*, *E. africanum* and *E. lasianthum* starts with the first rains, following the dry season (Aubréville 1959, Palmer & Pitman 1972, Pooley 1993, Arbonnier 2009).

The pods of *E. ivorense* and *E. suaveolens* open on trees around the beginning of the wet season (Aubréville 1959, Childes 1988, Arbonnier 2009). Pods remain attached to the tree for several months. It has been suggested that trees with persistent pods do not flower and therefore adopt a two-year fruiting cycle (Hawthorne 1995). *Erythrophleum suaveolens* produces fruits from 30 cm DBH (Diameter at Breast Height) in Cameroon and the fruiting becomes regular from 40 cm DBH (Kouadio 2009).

Table 2.1 Summary of the published data on phenology for the four African *Erythrophleum* species

Species	Study area	Leafs loss	New leaves	Flowers	Immature fruits	Mature fruits	Source
E. africanum	West Africa	-	Around flowering	Second part of the dry season	-	-	(Arbonnier 2009)
E. suaveolens	West Africa	-	-	March-April	-	-	(Aubréville 1950)
E. suaveolens	West Africa	-	-	February-May	-	-	(Arbonnier 2009)
E. suaveolens	Ivory Coast	-	-	February-May	-	-	(Aubréville 1959)
E. suaveolens	Ghana	-	-	End of the dry season	-	-	(Hawthorne 1995)
E. suaveolens	Cameroon	December-February	December-March	January-May	April-October	November-February	(Kouadio 2009)
E. ivorense	West Africa	-	-	June-August	-	-	(Poorter 2004)
E. ivorense	Liberia	-	-	May-September	-	-	(Voorhoeve 1965)
E. ivorense	Ivory Coast	-	-	June-October	-	-	(Aubréville 1959)
E. ivorense	Cameroon	-	-	July	-	-	(Aubréville 1970)
E. suaveolens	Gabon	July	Around October	-	-	-	(Chevalier 1916)
E. ivorense	Gabon	-	-	May-June	-	-	(Aubréville 1962)
E. africanum	Zimbabwe	July	October	September	-	-	(Childes 1988, Richer 2008)
E. lasianthum	South Africa (Natal)	-	-	September-November	-	June- August	(Palmer & Pitman 1972, Pooley 1993)

The double line is the separation between phenological data gathered north (above) and south (below) of the climatic hinge.

5.3 Pollination and dispersal

Erythrophleum species are hermaphroditic. The pollination is probably done by insects, as observed by Segers (2018) for *E. suaveolens* in Cameroon. The primary seed dispersion is ballochore: after a time of maturation, the pods open on tree and the seeds are ejected (Hawthorne 1995, Doucet 2003). Hawthorne (1995) also suggests that the seeds can be dispersed by wind during storm events. A secondary zoochoric dispersion has been observed for the two forest species *E. ivorense* and *E. suaveolens* (Poulsen *et al.* 2001, Kone & Lambert 2008, Kunz & Linsenmair 2008). Many primates have been identified as dispersing agents, such as gorillas (Gorilla gorilla gorilla Savage & Wyman; Petre personal communication), olive baboons (Papio anubis, Kunz & Linsenmair 2008), white-cheeked mangabey (Lophocebus albigena, Gray, 1850), chimpanzees (Pan troglodytes, Brumenbach, 1799, Poulsen *et al.* 2001) and cercopithecus diana (Cercopithecus diana, Liannaeus, 1758, Kone & Lambert 2008). These monkeys probably use seed mucilage as a substitute food during famine (Poulsen *et al.* 2001).

5.4 Seed dormancy and germination

Seeds of the *Erythrophleum* species are protected by very tough lignified seed coats, inhibiting rehydration (Netshiluvhi 1999, Kouadio 2009). The diaspores can remain in soil for several months to several years. This behaviour could explain the abundant regeneration of *E. suaveolens* in logging gaps and along the roadside, after the seed coat was damaged by logging equipment (Kouadio 2009). *Erythrophleum*'s germination is phanerocotyl and epigeal with fleshy cotyledons (de La Mensbruge 1966, Kouadio 2009, **Figure 2.3a**). The first leaves of seedlings are simply-pinnate (**Figure 2.3b**).

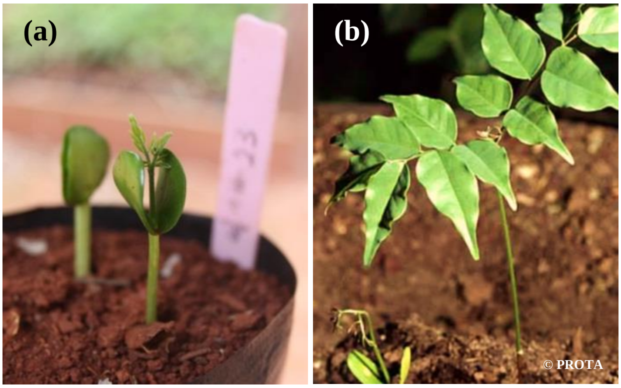

Figure 2.3 Germination (a) and juveniles (b) of *E. ivorense*

5.5 Growth

Growth in diameter differs between species (**Table 2.2**). The species occurring in the wettest habitat, *E. ivorense,* has the faster growth rate (0.65 cm/year), followed by *E. suaveolens* (0.45 cm/year), which occurs in moist and dry forests, and *E. africanum* (0.15 cm/year), in savanna.

Table 2.2 Published data on growth for the four African species of *Erythrophleum*

Species	AAG (cm/year)	n	Diameter range (cm)	Monito-ring period (year)	Study area	Method	Source
E. ivorense	0.65 ± 0,50	-	10 to 70	12	Ivory Coast	Circumference measurement	(Detienne *et al.* 1998)
E. suaveolens	0.45 ± 0,41	16	10 to 70	9	RCA	Circumference measurement	(Durrieu de Madron *et al.* 2000)
E. suaveolens	0.45 ± 0,09	38	10 to >100	6	Cameroon	Circumference measurement	(Kouadio 2009)
E. africanum	0.15	26	5 to 35	3	Zimbabwe	Circumference measurement	(Holdo 2006)

AAG: Average annual growth in diameter; n: number of trees; RCA: Central African Republic

6 Uses of Tali wood and sylvicultural practices

The two forest species, *E. ivorense* and *E. suaveolens,* are widely exploited for timber and traded under the same commercial name, Tali (ATIBT nomenclature). According to the International Tropical Timber Organization (ITTO, 2012), Cameroon is the main exporter of Tali, which is the second largest species exported as logs (125,000 m^3/year) and the 5th largest exported as sawn wood (18,000 m^3/year). The points discussed below relate to the wood properties and uses, the logging rules, the volume table and the artificial regeneration of *E. ivorense* and *E. suaveolens*.

6.1 Wood properties and uses

The wood of Tali is yellowish-brown to reddish-brown, darkening upon exposure. Its grain is coarse and interlocked. High risks of deformation and cracking require slow drying (CIRAD 2008). The wood is very hard and durable, being resistant to fungi, dry wood borers and termites (Aubréville 1959, Gerdat 1977, **Table 2.3**). The log of *E. suaveolens* is longer than the one of *E. ivorense* (10 m *vs*. 4-5 m), but according to forest operators, its wood is of lesser quality because of less uniform color. Logs are sometimes deformed and may have wetwood (Gerdat, 1977). The wood of Tali is used for heavy structures such as bridges, railway sleepers, terraces and industrial floors. It is also a good fuel and makes excellent coal (Burkill 1995).

6.2 Logging rules

In the African forest countries, two legal measures directly affect the logging of Tali. The first measure consists in fixing, for each country, the minimum cutting diameter limit (MCDL) which corresponds to the legal threshold below which trees can’t be exploited (Cameroon: MCDL = 50 cm, Central African Republic: MCDL = 60 cm (law n°08.022 of September 172008), Gabon: MCDL = 70 cm (l caw n° 16/01 of 31 December 2001), Republic of Congo: MCDL = 60 cm (law n°11/2002)). The second measure is based on the minimum recovery rates to be achieved during the cutting cycle. For example, in Cameroon, this rate must not be less than 50% after a 30 year cutting cycle (law 0511/D/MINFOF/SG/DF/BSJ, June 2010).

Table 2.3 Wood properties of the four African species of *Erythrophleum*

Properties		*E. ivorense*	*E. suaveolens*	*E. africanum*	*E. lasianthum*	*Source*
Specific gravity (g/cm^3)		0.774±0.058 n = 20	0.824±0.132 n = 7	0.852±0.036 n = 2	0,842 n = 1	Zanne et al., 2009
Specific gravity (kg/m^3)	12% moisture content	890 ± 7% n = 11	960 ± 9% n = 4	-	-	Gerdat 1977
Hardness *Chalais-Meudon*	12% moisture content	9.8 ± 6% n = 11	8.2 ± 43% n = 4	-	-	
Shrinkage (%)	Volumetric	13.7 ± 15% n = 11	15.1 ± 27% n = 4	-	-	
	Tangential	8.8 ± 13% n = 8	11.7 n = 1	-	-	
	Radial	5.3 ± 30% n = 8	6.1 n = 1	-	-	
Crushing strength (Mpa)	12% moisture content	79 ± 8% n = 8	79 ± 26% n = 4	-	-	
Static bending strength (Mpa)	12% moisture content	185 ± 13% n = 11	157 ± 17% n = 4	-	-	
Modulus of elasticity (Mpa)	12% moisture content	163.10^2 ± 13% n = 10	106.10^2 n = 1	-	-	
Durability	Fungi	Class 1- very durable		Very durable	-	CIRAD 2008 Arbonnier 2009
	Dry wood borers	Durable (risk limited to sapwood)		Durable	-	
	Termites	Class D - durable		Durable	-	
Treatability		Class 4 – not permeable		-	-	
Use class		Class 4 – in ground or fresh water contact		-	-	

n: number of samples, SD: standard deviation

6.3 Allometric equations

According to GlobAllomeTree (Henry *et al.* 2013), three allometric equations are available to quantify the volume of *E. ivorense* and *E. suaveolens* individuals (**Table 2.4**). However, the metadata associated with these equations are missing. Strictly speaking, allometric equations are only valid for a range of diameters identical to those of the trees used to build them and for area with similar environmental conditions. In addition, it should systematically be associated with the parameters used to calculate the confidence intervals of the estimates. In a recent study in Cameroon, Fayolle *et al.* (2013) proposed an allometric equation for *E. suaveolens* that meets these criteria. It is robust in an area covered by semi-deciduous forests on ferralitic soil, within a specific diameter range, and has clearly established parameters (**Table 2.4**).

Table 2.4 Allometric equations linking tree volume (V) to diameter (D) and/or height (H) according to GlobAllomeTree (http://www.globallometree.org, Henry et al., 2013).

Species	Allometric equation	Output (m^3)	n	Diameter range (cm)	Model quality	Study area	Source
E. ivorense	$V = 9{,}72 \times D^{2.46}$	Trunk vol.	-	-	-	Gabon	Bile Allogho (1999)
E. ivorense	$V = - 0{,}3 + 7{,}87 \times D^{2}$	Trunk vol.	-	-	-	Central African Republic (M'Baïki)	Ngabou (2011)
E. suaveolens	$V = - 0{,}0119 + 0.000428 \times D^{1.3979} \times H^{1.0433}$	Trading vol.	34	-	-	Nigeria	Akindele & LeMay (2006)
E. suaveolens	$V = 10{,}920 (\pm 1{,}03) \times D^{2{,}248(\pm 0{,}368)}$	Trunk vol.	12	50 to 140	$R^2 = 0{,}92$ RMSE = $1{,}6\ m^3$	Cameroon (South-East)	Fayolle *et al.* (2013)

n: number of trees; vol: volume

6.4 *Artificial regeneration and plantation*

The production of trees in nursery requires to break the dormancy of the seeds. In a study on *E. suaveolens*, Kouadio (2009) shows that dormancy can be broken by immersing the seeds in 60% sulphuric acid for 40 minutes.

After the germination, the inoculation of rhizobium (*Bradyrhizobium spp.*) has a positive effect on the seedlings growth (Diabate *et al.* 2005). After four months in the nursery, the inoculated seedlings grew higher in height and diameter compared to the non-inoculated ones (37-40% higher for *E. ivorense* seedlings and 20-30% higher for *E. suaveolens*). *Erythrophleum ivorense* is particularly well adapted to clear-cutting installations, which confirms its light-demanding temperament (Koumba Zaou *et al.* 1998). In Cameroon, 100% recovery rates of *E. suaveolens* seedlings have been observed two months after their plantation in logging gaps (Kouadio, 2009). The plantation of Tali is therefore practicable, however, its profitability has yet to be demonstrated (Doucet 2003).

7 Other uses of *Erythrophleum* species

Erythrophleum species are well known for the properties of their bark, wood and leaves which contain a toxic agent, the Erythrophlein. Depending on the dosage, decoctions of these organs may be therapeutic or toxic (Burkill 1995). Bark decoction was used for trial by ordeal (Aubréville 1959, Palmer & Pitman 1972, Hawthorne 1995). Nowadays, *Erythrophleum* extracts are used as poison or repellent against all kinds of animals, from rodents to stray cattle (Palmer & Pitman 1972, Burkill 1995, Hawthorne 1995, Arbonnier 2009). Extracts were also tested as low environmental impact products for the control of pathogen and pests (Akinpelu *et al.* 2013).

Erythrophleum species are mainly used in traditional pharmacopoeia. For example, the bark of *E. suaveolens* is indicated for the treatment of convulsions, pain, heart problems and edema caused by nematodes (Burkill 1995). Decoctions and infusions of *E. ivorense*, *E. suaveolens* are also used for their emetogenic, laxative and anti-rheumatic properties (Burkill, 1995). The antioxidant properties of the *E. africanum* bark justify its wide use for dental treatment (Brice *et al.* 2011). The extensive use of *E. lasianthum* bark in traditional medicine is one of the causes of the visible decline of the species. Since 2009, *E. lasianthum* has been listed on the Red List of South African Plants as "Near Threatened". Scientists are drawing inspiration from these traditional uses and studying the properties of *Erythrophleum*'s intrinsic molecules for agri-food or pharmaceutical purposes (Akinpelu *et al.* 2013, Fadeyi *et al.* 2013).

3

The niche evolution within *Erythrophleum*

1 Preamble

Genetic and phylogenetic approaches have been frequently used to study the diversification of African tree clades (Hardy *et al.* 2013). However, the environmental space occupied by congeneric species or intra-specific gene pools has been barely quantified (but see Couvreur *et al.* 2011 for *Isolona* and *Monodora* (Annonaceae), Holstein & Renner 2011 for *Coccinia* (Cucurbitaceae)). Quantifying the ecological divergence between related species or gene pools is fundamental to properly support the role of ecology in diversification (Graham *et al.* 2004). At the species level, ecological divergence is one of the baseline evidence to support ecological speciation (Rundell & Price 2009, Nosil 2012). At the gene pool level, ecological divergence highlights local adaptation driven by the environment.

The *Erythrophleum* genus is extremely widespread across tropical Africa (**Chapter 2**). In this chapter, we used species distribution models (SDMs) to determine the bioclimatic constraints on the distribution of the *Erythrophleum* species across tropical Africa, and of *E. ivorense* and *E. suaveolen*s gene pools in the Upper and Lower Guinean Subcentres. Then, we combined the available phylogenetic data with information on ecological niche divergence to explore the history of niche evolution within the genus. 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).

This study has been published in *Plant ecology and Evolution*: Gorel, A.-P., Duminil, J., Doucet, J.-L. and Fayolle, A. 2019. *Ecological niche divergence associated with species and populations differentiation in* Erythrophleum *(Fabaceae, Caesalpinioideae)*. Plant Ecol. Evol. 152: 41–52.

2 Methods

2.1 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). Before modelling, we trimmed the occurrence 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 distribution.

2.2 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 Subcentres (Hijmans *et al.* 2005). To reduce collinearity between environmental variables and the risk of overfitting, we used a subset of nine weakly correlated variables ($r_{Pearson} < 0.70$, the Pearson correlation table is given in electronic appendix 1). The nine variables retained were altitude (alt, in m), annual mean temperature[6] (Bio1, in °C x 10), isothermality (Bio3, unit-less), temperature annual range (Bio7, in °C × 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).

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[6] Calculated as the maximum temperature of the warmest month minus the minimum temperature of the coldest month

2.3 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 other 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 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[7] 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 (ORmtp), the True Skill Statistic (TSS, Allouche et al. 2006), the AUCtest and the AUCdiff. The AUC were calculated with the full set of background data used for model's calibration. The AUCtest 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).

2.4 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.

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[7] The regularization multiplier affects how closely-fitted the output distribution is – a smaller value than the default of 1.0 will result in a more localized output distribution.

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 pools tolerate exactly the same environmental conditions and have an equivalent set of environmental conditions 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).

3 Results

3.1 Predicted 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 3.1**). For evaluating the robustness of 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 3.1**).

Table 3.1 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 AUCtest: Area Under the receiver operating characteristic Curve calculated with a test sample; AUCdiff: the difference between AUC values based on training localities and AUCtest; ORmtp: 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. ivorense*, *E. ivo Cn*: northern Central Africa *E. ivorense*, *E. ivo Cs*: southern Central Africa *E. ivorense*, *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**				
	E. ivorense	***E. suaveolens***	***E. africanum***	***E. ivo* Cs**	***E. ivo* Cn**	***E. sua* Cs**	***E. sua* Cn**	***E. sua* W**
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

At the species level, the modelled distribution for each species accurately predicted the observed species' distribution (**Figure 3.1a**). The distribution of *E. ivorense* was restricted to the wet forests in the Upper and Lower Guinean Subcentres and thus showed an interruption in the Dahomey gap. *Erythrophleum suaveolens* had a wide distribution that extended over the entire Guineo-Congolian Centre, with the exception of the area occupied by *E. ivorense*, and the adjacent Transition Zones (Guineo-Congolian/Zambezian and the Guineo-Congolian/Sudanian). The model did not predict a high probability of presence of *E. suaveolens* in the Zambezian Centre except in southern Tanzania and northern Mozambique. The predicted distribution of *E. suaveolens* was also largely distinct from that of *E. africanum* except in the Guinean-Congolese/Sudanian and Guinean-Congolese/Zambezian Transition Zones where the distributions overlapped. The predicted distribution of *E. africanum* was restricted to the savannas of the Sudanese and Zambezian Centres and to the Transition Zones around the Guineo-Congolian Centre.

At the gene pool level, the models suggest overlapping distributions for the *E. ivorense* gene pools (**Figure 3.1b**) but distinct distributions for the *E. suaveolens* gene pools (**Figure 3.1c**). The *E. ivo Cn* distribution covered almost the whole distribution of *E. ivorense* and extended to the geographic area occupied by *E. ivo W*. The distribution of *E. ivo Cs* was restricted to the low coastal plain of the Gabon estuary with a relative low probability of presence that extended along the coast. The distributions of *E. sua W*, *E. sua Cn* and *E. sua Cs* were largely distinct (**Figure 3.1c**). *E. sua W* spanned the Upper Guinean Subcentre, the Dahomey Gap and the northern part of the Lower Guinean Subcentre. In central Africa, the 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.

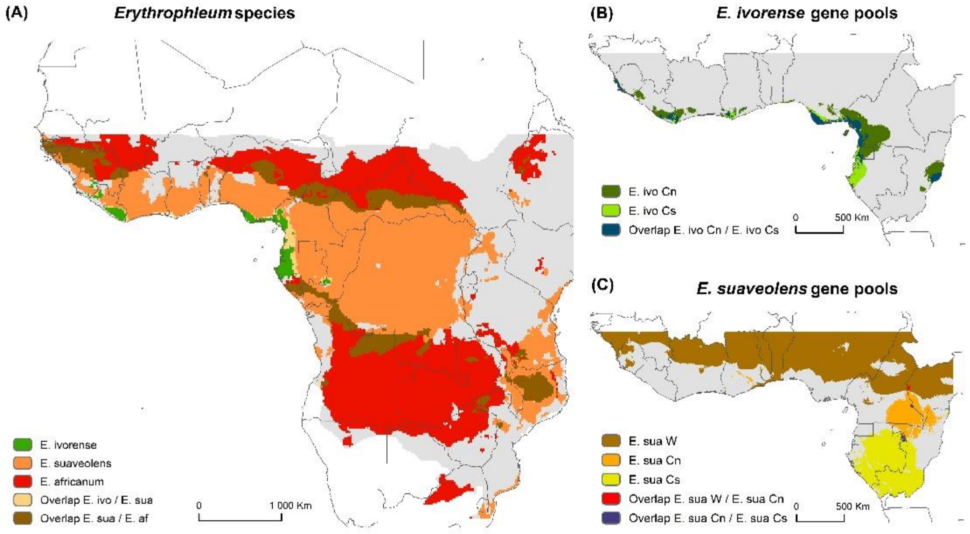


Figure 3.1 Predicted distributions for *Erythrophleum* species (a), *E. ivorense* (b) and *E. suaveolens* gene pools (c). Suitable areas were identified for the three species and the five gene pools using a suitability threshold that was identified by maximizing the sum of the sensitivity (true positive rate) and specificity (true negative rate). Overlap between pairs of species and pools are also given.

3.2 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 3.2**). Annual precipitation and annual temperature range explain together more than 40% of the distribution of each species (**Table 3.2**). 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. ivorense* was found at higher annual precipitation (optimum close to 3900 mm). *Erythrophleum ivorense* 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, **Figure 3.2**, **Table 3.2**). The distribution of *E. ivorense* 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 3.2**).

In the Upper and Lower Guinean Subcentres, the distribution of *E. ivorense* and *E. suaveolens* gene pools showed contrasting responses to the environment (**Table 3.2**). Precipitation of the warmest quarter was the most important constraint on the 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 distribution of *E. sua Cs* (15.5%). 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, **Figure 3.2**). 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) with highest suitability at values close to 8°C. The precipitation seasonality (22.9%) and annual precipitation (17.5%) together shape the distribution of *E. sua Cn* (**Table 3.2, Figure 3.2**). Areas with precipitation seasonality around 20 mm and with an annual precipitation of 850 mm showed highest suitability.

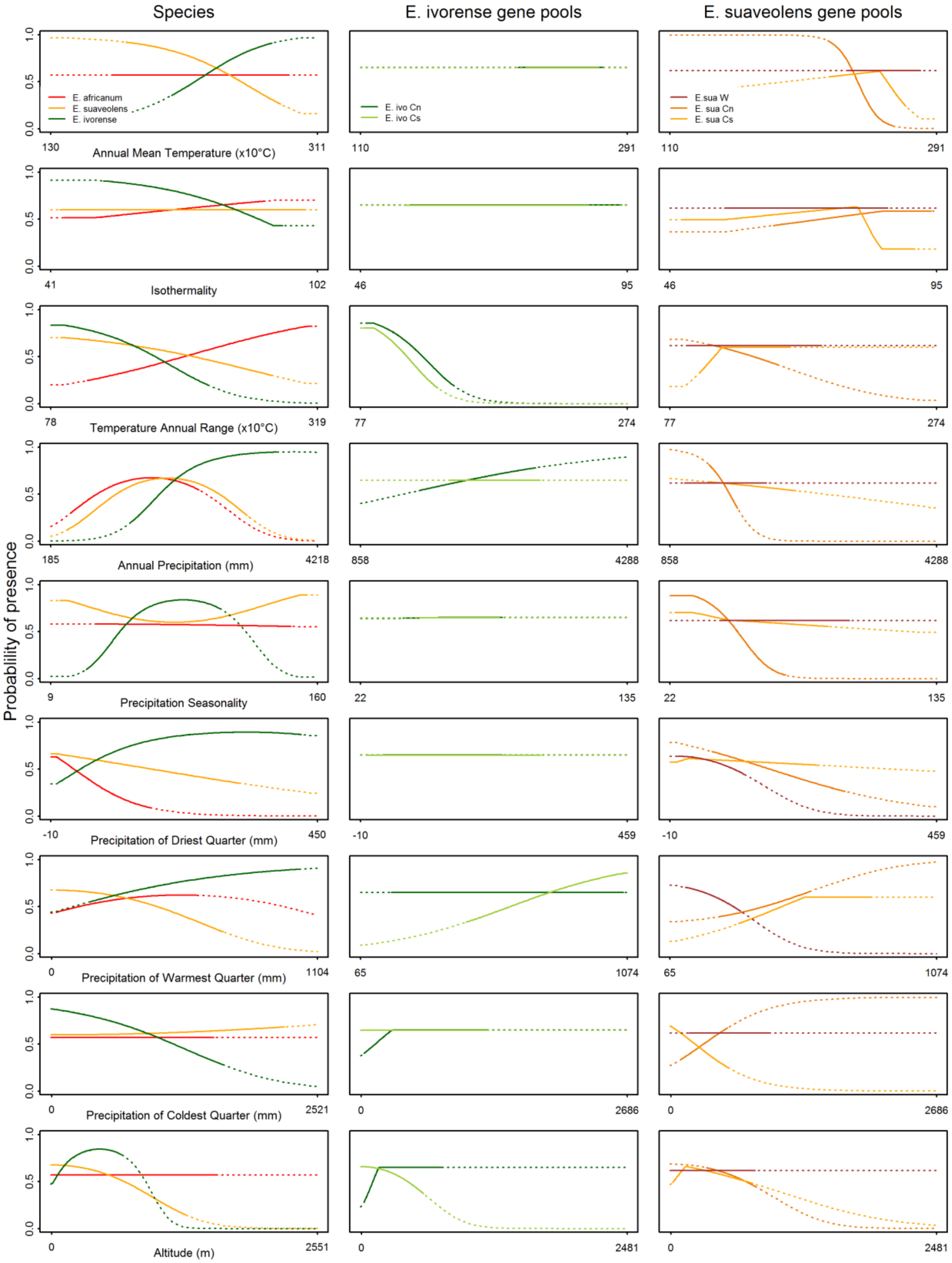


Figure 3.2 Response curves to the 8 retained environmental variables for each species (left panels), *E. ivorense* gene pools (central panels) and *E. suaveolens* gene pools (right panels). Response curves are based on the SDMs and show the ranges (x axis) in environmental conditions that are more favorable for the distribution of the species. The predictions are shown on the whole environmental gradient over the study area, including sites/areas outside the environmental space used (dotted line).

Table 3.2 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. ivorense*, *E. ivo Cn*: northern Central Africa *E. ivorense*, *E. ivo Cs*: southern Central Africa *E. ivorense*, *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	***E. ivorense***	***E. suaveolens***	***E. africanum***	***E. ivo Cs***	***E. ivo Cn***	***E. sua Cs***	***E. sua Cn***	***E. sua W***
Annual Mean Temperature	C = 0.0 P = 5.3	C = 5.3 P = 11.0	C = 0.0 P = 0.0	C = 0.3 P = 0	C = 0 P = 0	C = 1.5 P = 11.1	C = 3.2 P = 18.6	C = 0 P = 0
Isothermality	C = 0.3 P = 2.5	C = 0.0 P = 0.0	C = 0.2 P = 5.1	C = 0 P = 0	C = 0 P = 0	C = 3.5 P = 4.8	C = 40.3 P = 0	C = 0 P = 0
Annual Temperature Range	**C = 33.0** **P = 13.1**	**C = 33.9** **P = 12.8**	**C = 26.3** **P = 31.3**	**C = 26** **P = 43.3**	**C = 36** **P = 46.5**	C = 7.5 P = 3.2	C = 0 P = 0.7	C = 0 P = 0
Annual precipitation	**C = 29.9** **P = 40.9**	**C = 23.9** **P = 32.7**	**C = 18.1** **P = 18.4**	C = 2.3 P = 0	**C = 17.2** **P = 5**	C = 0.6 P = 3.8	**C = 17.5** **P = 33**	C = 0 P = 0
Precipitation seasonality	C = 3.6 P = 7.8	C = 4.0 P = 6.2	C = 0.2 P = 0.2	C = 0 P = 0	C = 0.2 P = 0	C = 1.2 P = 4.4	**C = 22.9** **P = 29**	C = 0 P = 0
Precipitation of Driest Quarter	C = 1.4 P = 6.7	C = 0.5 P = 2.7	**C = 50.1** **P = 42.2**	C = 0 P = 0	C = 27.1 P = 0	C = 0.9 P = 0	C = 3.5 P = 1.9	**C = 19.3** **P = 39.7**
Precipitation of Warmest Quarter	C = 16.1 P = 0.4	C = 6.0 P = 9.0	C = 3.5 P = 2.8	**C = 64.7** **P = 32.3**	C = 0 P = 0	**C = 15.5** **P = 26.7**	C = 2.5 P = 4.7	**C = 80.7** **P = 60.3**
Precipitation of Coldest Quarter	C = 2.9 P = 3.3	C = 1.4 P = 0.2	C = 0.6 P = 0.0	C = 0 P = 0	C = 8.4 P = 29.4	**C = 62.2** **P = 40**	C = 0.5 P = 6	C = 0 P = 0
Elevation	**C = 12.8** **P = 20.1**	**C = 25.0** **P 25.3**	C = 1.0 P = 0.0	**C = 6.6** **P = 24.4**	**C = 11.2** **P = 19.1**	**C = 7** **P = 6.1**	**C = 9.6** **P = 6.1**	C = 0 P = 0

3.3 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 3.3**).

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 no 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 3.3**), 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. ivorense* gene pools tended to be more similar than expected by chance and provided an evidence for niche conservatism (**Table 3.3**). 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 3.3**).

Table 3.3 Niche overlap and similarity between pairs of *Erythrophleum* species and gene pools. Niche overlap (D) and results of 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. D_{comp} 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. ivorense, E. ivo Cn*: northern Central Africa *E. ivorense*, *E. ivo Cs*: southern Central Africa *E. ivorense*, *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**	
	Niche Overlap (D)	$\mathbf{D_{comp}}$	**Similarity**	$\mathbf{D_{comp}}$	**Similarity**	$\mathbf{D_{comp}}$	**Similarity**	$\mathbf{D_{comp}}$	**Similarity**
***E. ivorense* – *E. suaveolens* (Null)**	0.26	-	-	0.90 ± 0.01	Less similar $P <=0.01$	0.85 ± 0.01	Less similar $P <=0.01$	0.81 ± 0.01	Less similar $P <=0.05$
***E. suaveolens* – *E. ivorense* (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 $P <=0.001$
***E. suaveolens*– *E. africanum* (Null)**	0.47	-	-	0.86 ± 0.02	Less similar $P <=0.01$	0.84 ± 0.02	Less similar $P <=0.01$	0.80 ± 0.03	Less similar $P <=0.01$
***E. africanum* – *E. suaveolens* (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 $P <=0.001$
***E. ivo Cs* – *E. ivo Cn* (Null)**	0.53	0.51 ± 0.02	More similar $P <=0.001$	0.54 ± 0.01	More similar $P <=0.001$	0.57 ± 0.01	More similar $P <=0.001$	-	-
***E. ivo Cn* – *E. ivo Cs* (Null)**		0.50 ± 0.01	More similar $P <=0.001$	0.49 ± 0.01	More similar $P <=0.001$	0.49 ± 0.02	More similar $P <=0.001$		
***E. sua Cs* – *E. sua Cn* (Null)**	0.26	0.66 ± 0.01	ns	0.65 ± 0.01	ns	0.61 ± 0.01	Less similar $P <=0.001$	-	-
***E. sua Cn* – *E. sua Cs* (Null)**		0.80 ± 0.01	Less similar $P <=0.001$	0.79 ± 0.01	Less similar $P <=0.001$	0.71 ± 0.01	Less similar $P <=0.001$		
***E. sua W* – *E. sua Cn* (Null)**	0.09	0.66 ± 0.01	More similar $P <=0.001$	0.65 ± 0.01	More similar $p<=0.01$	0.61 ± 0.01	Less similar $P <=0.001$	-	-
***E. sua Cn* – *E. sua W* (Null)**		0.52 ± 0.02	More similar $P <=0.01$	0.56 ± 0.03	ns	0.60 ± 0.03	Less similar $P <=0.05$		

4 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, Couvreur *et al.* 2011, Holstein & Renner 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. ivorense* 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/cm^3) 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 (Markesteijn & Poorter 2009). In contrast, the wet forest species, *E. ivorense* shows the opposite suite of traits and the highest growth rates (leaves: 8.5 × 4 cm; wood density: 0.774 ± 0.058 g/cm^3; 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 favour 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 drier climates of the mid-Pliocene (Liddy *et al.* 2016) could have boosted the divergence of *E. africanum* from the common ancestor of *E. suaveolens* and *E. ivorense*. Between *E. suaveolens* and *E. ivorense*, the divergence date (c. 650 ka, Duminil *et al.* 2015) is concomitant with the climatic oscillations of the Pleistocene (Johnson *et al.* 2016). 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. ivorense*, however, a general conclusion on the role of ecology into genetic diversification is more difficult to propose. The divergence dates of gene pools are concomitant with arid phases during the Pleistocene climatic oscillations (Collins *et al.* 2014, Lézine *et al.* 2019). The climate-driven contractions of forests 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). *Erythrophleum 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.* 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).

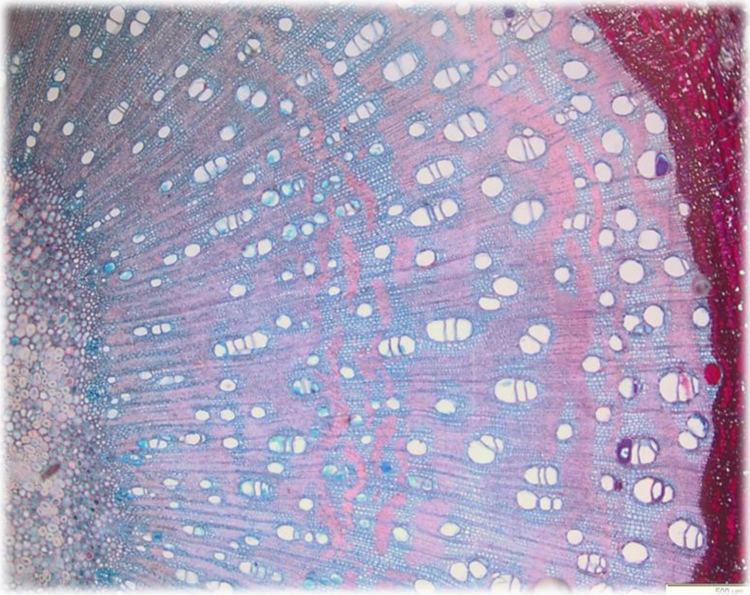
Within *E. ivorense*, the similarity tests support niche conservatism, rejecting ecological divergence and supporting the forest refuge hypothesis. Interestingly, the genetic differentiation within *E. ivorense* has been identified to be lower than the genetic differentiation within *E. suaveolens* (Duminil *et al.* 2013, 2015). To interpret these results, Duminil *et al.* (2015) suggested that the distribution of *E. ivorense* has been less fragmented than that of *E. suaveolens*, either because glacial refugia of *E. ivorense* 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. ivorense* can also be an alternative explanation to the lower genetic differentiation. *Erythrophleum ivorense* 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 ivorense* 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 had 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 (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).

In this chapter, we provided evidence that supported the substantial role of climate in niche evolution, and speciation, within *Erythrophleum* genus in Africa. *Erythrophleum* has managed to adapt to pronounced climatic shifts, resulting in a vast distribution encompassing biomes, from the wet forest to the dry forest and the savanna. Niche evolution along rainfall gradients is probably a key mechanism in the diversification of the tropical African flora, since similar patterns of niche partitioning have been reported for many other genera, such as *Diospyros* (Ebenaceae, White 1978), *Afzelia* (Fabaceae, Donkpegan 2017) and *Guibourtia* (Fabaceae, Tosso 2018). However, we were also confronted with the limits of the SDMs. 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 the niche along relevant environmental axes is a challenge and our results strongly depend on the environmental factors tested (and available). For instance, even if climate and specifically rainfall has been found as a main correlates of floristic diversity in multiple studies, conclusions about the role of climate in the diversification processes within *Erythrophleum* genus may be confounded by the correlations between climate and other environmental factors, such as soil fertility (Swaine 1996) and mycorrhizal associations (Gerz *et al.* 2018). Therefore, within lineages, dissecting the species strategies and functional traits would be useful to confirm the niche evolution along a particular gradient, and also, to understand the mechanistic underpinnings of ecological transitions (Westoby 1998, Wiens & Donoghue 2004).

4

The functional understanding of niche evolution

Part I: Hydraulics and wood traits



1 Preamble

Previously, we used species distribution models (SDM) and provided evidence for the substantial role of climate, specifically rainfall-aridity gradients, in niche evolution and diversification within the genus *Erythrophleum* (**Chapter 3**). However, SDM do not allow the identification of the changes in ecological strategies and traits that underpin niche evolution. In this chapter, we report the results of an integrated eco-physio-morphological approach developed to examine the evolutionary changes that allowed *Erythrophleum* to adapt to drier environments.

We specifically studied *Erythrophleum ivorense* and *E. suaveolen*s, the two sister species, morphologically similar, often confused in the field, and traded under the same commercial name, Tali (**Chapter 2**). The two species occupy contrasting forest types and rainfall conditions (**Chapter 3**). *Erythrophleum ivorense* is restricted to the coastal wet evergreen forests of the gulf of Guinea. *Erythrophleum suaveolens* is widespread across tropical Africa, encompassing the moist forests of the Guineo-Congolian Region and the savannas of the Sudanian and Zambezian Regions.

We examined between-species differences in tree hydraulics including vulnerability to embolism, wood water content and capacitance, and we determined the underlying wood traits, especially vessel-associated traits. A common garden was specifically used to test whether differences in growth and wood traits observed in the natural habitat are maintained under the same environment.

This study has been published in *Biotropica*: Gorel, A.-P., Steppe, K., Beeckman, H., De Baerdemaeker, N. J. F., Doucet J.-L., Ligot, G., Daïnou, K. and Fayolle, A. 2019. *Testing the divergent adaptation of two congeneric tree species on a rainfall gradient using eco-physio-morphological traits*. Biotropica btp.12646.

These results were also part of a methodological paper submitted in Annals of Forest Science and entitled “Triple analysis of xylem vulnerability to drought-induced embolism uniting acoustic vulnerability, hydraulic capacitance and xylem anatomy” (De Baerdemaeker, Hubeau *et al.*, in prep.).

2 Methods

2.1 Study sites

Data and samples were collected in two sites in southern Cameroon: the Ma’an site, east of the Campo-Ma’an National Park, natural habitat of *E. ivorense* (around 2°22’N and 10° 37’E) and the Mindourou site, east of the Dja Faunal reserve, natural habitat of *E. suaveolens* (around 3° 33’N and 13°14’E, **Figure 4.1**).

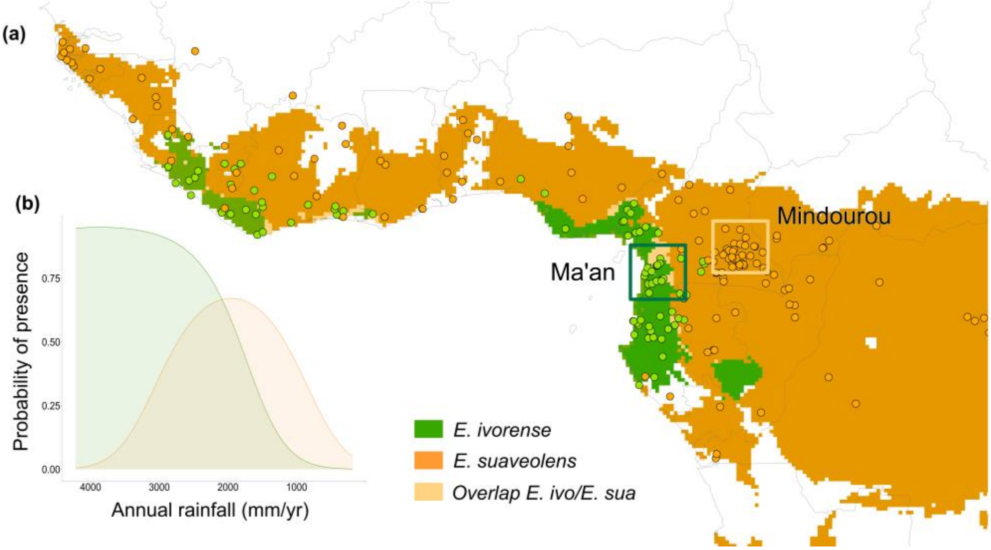


Figure 4.1 Species distribution and study sites. Predicted distribution in Upper and Lower Guinea (a) and response curve (probability of presence) along the rainfall gradient (b) of the two sister species *Erythrophleum ivorense* (in green) and *E. suaveolens* (in orange). The average rainfall has been extracted from “bioclim” data (BIO12, Hijmans *et al.* 2005) and corresponds to the average of the rainfall measured over a 30-year period (from 1970 to 2000). Note that the distribution of *E. suaveolens* is much larger across southern and eastern Africa, but genetic information is lacking (Duminil, Heuertz & Hardy 2010). The location of the two study sites Ma’an and Mindourou in Cameroon, corresponding to the natural habitat of *E. ivorense* and *E. suaveolens*, respectively, are indicated on the map (colored squares). The common garden experiment was set up at the Mindourou site, *i.e.* in the natural habitat of *E. suaveolens*. The occurrence data used to model the distribution of the species overlaid on the map. The predicted distributions and the response curves result from species-specific distribution modeling (Gorel, Duminil, *et al.* 2019).

Forests in the Ma'an site are assigned to Wet Central Africa (Fayolle *et al.* 2014, hereinafter designated as "wet forest") and correspond to lowland evergreen forests (Letouzey 1985). The annual rainfall is up to 2070 mm with two periods of maximum rainfall separated with drier periods without real water deficit (monthly precipitation no less than 45 mm, **Figure 4.2**). The mean annual temperature is 23.3°C (Hijmans *et al.* 2005). Forests in the Mindourou site are assigned to Moist Central Africa (Fayolle *et al.* 2014, hereinafter designated as "moist forest") and have been previously described as a transition type between the evergreen and the semi-deciduous forests with a canopy dominated by species of the Meliaceae, Malvaceae and Ulmaceae families indicating a strong floristic affinity with the semi-deciduous forests (Letouzey, 1985). The annual rainfall is up to 1640 mm with a pronounced dry season of almost three months (December to February) and the mean annual temperature is 23.2 °C (**Figure 4.2**). In both sites, the topography is undulating, with elevation varying between 600 and 800 m, and between 500 and 650 m, in the Ma'an and Mindourou sites, respectively. The geological substrate consists of volcanic intrusions and metamorphic rocks, and soils are generally attributed to Ferralsols (Jones *et al.* 2013).

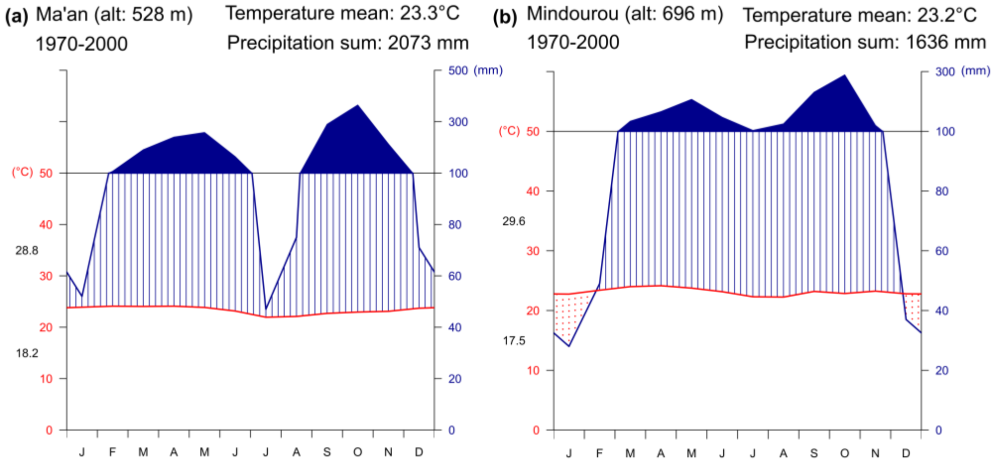


Figure 4.2 Climate diagrams. Walter-Lieth climate diagram of monthly average temperature (red solid line) and precipitation (blue solid line) for the Ma'an site (a), natural habitat of *E. ivorense* and the Mindourou site (b), natural habitat of *E. suaveolens*. The diagrams were constructed with the "Wordclim" data (Hijmans *et al.* 2005)

In the Mindourou site, the two study species were also grown in a common garden. Seeds were collected from multiple mother trees in north-west Gabon for *E. ivorense* and from four provenances for *E. suaveolens*, but we restricted our analyses to the provenance close to the Mindourou site. Juveniles were raised in a nursery for six months prior to plantation in 2008. The common garden experiment followed a randomized block design (20 randomized blocks, with 20 trees per block). Each block contained a single offspring per mother tree, planted at distances of 10 m.

2.2 Field sampling

In the natural habitat, branch and stem samples were collected during daytime in March 2016 on felled trees (day of year (DOY) 71 and 72 for *E. ivorense* (n =9) and DOY 90 and 92 for *E. suaveolens* (n=5). Average height (± SD) was 33.00 (± 4.19) m for *E. ivorense* in Ma'an and 34.08 (± 1.42) m for *E. suaveolens* in Mindourou, and these trees can be considered as mature trees.

In the common garden, branch samples were collected during March 2015 on individuals *E. ivorense* (n=8) and *E. suaveolens* (n=7, DOY 68-72). We selected individuals with the best growth rate, no liana infestation and crown dieback since 2008. Average height (± SD) was 12.25 (± 3.15) m for *E. ivorense* and 9.70 (± 3.53) m for *E. suaveolens*, and these 7 year old trees can be considered as juvenile trees.

To quantify hydraulic traits, branches from the natural habitat were cut under water. The cut end was put immediately into a small vial filled with water and the branch was enclosed in a wet and opaque plastic bag. The branch samples were conserved in a cool box until measurements. These precautions were taken to keep the branch segments in a hydraulic equilibrium state from the field to the laboratory. Excised branches of *E. ivorense* and *E. suaveolens* were transported on DOY 75 and DOY 97, respectively, to the Laboratory of Plant Ecology, Ghent University (Belgium).

To quantify wood traits, branch samples were collected between 10 and 20 cm from the apex and stem samples were collected at breast height (1.30 m). Samples were stored in 50% ethanol until measurements in laboratory of the Wood Biology Service of the Royal Museum for Central Africa (Belgium).

2.3 Hydraulic traits

In the laboratory, branches from three individuals (out of the branch sampled) per species were selected on uniformity in length (average (± SD)) was 80 ± 11 cm for *E. ivorense* and 81 ± 4.1 cm for *E. suaveolens*) and diameter (9.2 ± 1.8 mm for *E. ivorense*; 8.7 ± 0.8 mm for *E. suaveolens*) to minimize statistical sampling variability. Branches were analyzed from DOY 75-76 for *E. ivorense* and from DOY 97-100 for *E. suaveolens*.

During the preparation steps, the experimental room was darkened with an artificial green light to diminish photosynthesis and transpiration (De Baerdemaeker *et al.* 2017). For each species, three branches were placed in a custom-built holder and equipped with a broadband point-contact acoustic emission (AE) sensor (KRNBB-PC, KRN Services, Richland, WA, USA) and a dendrometer (DD-S, Ecomatik, Dachau, Germany). Three other branches were placed on continuous weighing scales after removing the leaves and covering the created wounds with petroleum jelly. For

AE-selected branches, all the leaves were wrapped in aluminum foil to equalize the dehydration procedure. Wrapping leaves in aluminum foil allowed the determination of stem water potential (ψ, MPa) with the pressure chamber (PMS Instrument Company, Corvallis, OR, USA). The AE sensor and the dendrometer were installed directly onto the xylem surface by removing two sections of bark (1.5 x 0.5 mm). To avoid evaporation and provide good acoustic contact vacuum grease was applied between the AE sensor tip and the xylem surface, while petroleum jelly was smeared against the exposed section for the dendrometer to similarly avoid evaporation. At the end of the preparation steps, the water filled vial was removed from both sets of branches. The first measure of stem water potential was close to zero indicating no sign of premature drought stress and no trace of gel or tylose clogging of vessels was detected on optical micrographs.

Collected AE signals were used to construct an acoustic vulnerability curve (VC_{AE}, Vergeynst *et al.* 2015, De Baerdemaeker *et al.* 2017). The AE signals were cumulated over the measurement period, and averaged over 5 minutes. The endpoint of the VC_{AE} was based on the local maximum in the third derivative, following the strongest decrease in the first derivative. Cumulative acoustic emissions were then rescaled between zero and the defined endpoint to obtain a relative percentage of embolism-related AE (%). The continuous water potential x-axis of the VC_{AE} was obtained from a segmented linear regression relation between point measurements of xylem water potential, and xylem shrinkage monitored by the dendrometers (De Baerdemaeker *et al.* 2017). Thresholds corresponding to the onset of embolism (AE_{12}), 50% embolism-related AE (AE_{50}), full embolism (AE_{88}), and endpoint of the VC_{AE} (AE_{100}) were assessed as well (De Baerdemaeker *et al.* 2017).

In order to normalize weight loss data to wood volumetric water content (VWC, kg/m^3), ~5 cm wood samples were taken at the start and the end of the dehydration experiment of both sets of branches. Diameter, length and weight were measured. Each sample was then oven dried (100°C) till constant mass, after which the respective quantities were re-measured. Because water potential data is only obtained from the AE branches, the AE wood samples are used to calculate VWC by re-scaling weight loss data between initial and final water content of the samples (Vergeynst, Dierick, *et al.* 2015). Samples collected from the scale-selected branches were used as a reference to validate that both sets of branches dehydrated in a similar manner. The resulting desorption curve is obtained by plotting wood VWC against the continuous Ψ axis. Within this curve three regions of interest are determined based on three defined breakpoints, calculated via the Segmented package (Muggeo 2008) in the R software (R Core Team 2016). The zone between the first and second breakpoint is known as the initial phase or capillary water phase. The zone between the second and third breakpoint is the elastic phase or phase I, and the zone after the third breakpoint till the AE_{100} is the inelastic phase or phase II (Vergeynst, Dierick, *et al.* 2015, Epila, Baerdemaeker, *et al.* 2017). The hydraulic capacitance, defined as the amount of water released from the tissue into the xylem per unit decrease in ψ, is then calculated for the distinct phases as the slope of the linear regression between VWC and Ψ (Vergeynst, Dierick, *et al.* 2015).

Acoustic vulnerability curves and desorption curves were averaged between the different samples. VC_{AE}s are fitted with the *smooth.spline* function in the stats package.

2.4 Wood traits

On branch and stem samples, thin transverse and tangential sections of 16 µm thickness were cut with a semi-automated microtome (Microm HM 440 E, GMI, Ramsey, MN, USA). The sections were stained in Safranin/Alcian blue mixture, dehydrated in an ethanol series (50%, 75%, 96%) and mounted in Euparal. Sections were transformed into images using an automated OLYMPUS BX60 microscope with a motorized positioning stage (Märzhäuser GmbH & Co. KG, In der Murch 15, 35579 Wetzlar, Germany).

Transverse sections were used to measure tangential vessel diameter, vessel density and vessel grouping index (ratio of total number of vessels to total number of vessel groupings; Scholz *et al.* 2013). We also quantified the proportion of vessel lumen, fibre, axial and radial parenchyma. On branch sections, these measurements were done on 0.14 mm² quadrats systematically distributed from the pith to the bark, in order to include radial variation in wood traits. For stem sections, measurements were done on two quadrats of 9.40 mm². Intervessel wall thickness and fiber wall thickness (measured as the double wall between two adjacent fibers) were also measured at higher magnification. Conduit wall reinforcement was calculated by determining the wall thickness (t) to conduit wall span (b) ratio $(t/b)_h^2$ as described by Hacke *et al.* (2001). On tangential sections, we measured the horizontal pit membrane diameter at its widest point (sensu Scholz *et al.* 2013) but only for branch samples from natural habitat. Images were processed with ImageJ 1.47v software.

To test for between-species differences in wood traits, we used linear mixed models fitted with the lme4 R package (Pinheiro *et al.* 2017). Random effects were included in the models to account for individual variability. The best model for each wood trait was selected based on the Akaike Information Criterion (AIC). We first identified the best random structure and then the best fixed structure following Zuur *et al.* (2009). For the stem samples, the full model estimated wood trait (*WT*) of the individuals (*i*) belonging to each species (*sp*), with a random intercept (α, eq. 1). For the branch samples, except for the fiber wall thickness, the conduit wall reinforcement and the pit membrane diameter for which the eq. 1 has been used, the effect of the distance to the pith (*dist*) and a random slope (β) have been added in order to consider radial variation in wood anatomy (eq. 2).

$$WT_{i,sp} = a_{sp} + \alpha_{i,sp} + \varepsilon_{i,sp} \qquad \text{eq. 1}$$

$$WT_{i,sp} = a_{sp} + b_{sp} \times \text{dist} + \alpha_{i,sp} + \beta_{i,sp} \times \text{dist} + \varepsilon_{i,sp} \qquad \text{eq. 2}$$

with a_{sp} and b_{sp} as fixed parameters, $\alpha_{i,sp}$ and $\beta_{i,sp}$ as random parameters, and $\varepsilon_{i,sp}$ as the random error.

2.5 Growth

In the natural habitat of the two species, diameter was monitored yearly since 2013 on a large number of trees covering the species diameter range (*E. ivorense* n = 46, *E. suaveolens* n = 192). The monitoring of tree growth was done on permanent transects in unlogged forest. The diameter measurements were done at breast height (1.30 m). For trees with stem irregularities at breast height, the point of measurement was raised 1 m above the deformations. The diameter was measured with a tape to the nearest millimetre and a permanent mark was placed on tree trunk to ensure that diameter was monitored every year at the same height. Annual diameter increment was calculated over a 3 to 4-year period. Average initial diameter (± SD) was 61.64 cm (± 24.01) for *E. ivorense* and 64.03 cm (± 26.70) for *E. suaveolens*.

In the common garden experiment, diameter was monitored yearly (*E. ivorense* n=76, *E. suaveolens* n=167). The DBH was measured with a tape to the nearest millimeter and a permanent mark was placed on tree trunk to ensure that diameter was monitored every year at the same height. Annual diameter increment was calculated since 2010 over a 4-year period (from June 2010 to June 2014). Average initial diameter (± SD) was 29.32 cm (± 10.36) for *E. ivorense* and 24.55 cm (± 8.24) for *E. suaveolens*.

Between-species differences in growth have been analyzed with one-way ANOVA. To account for the ontogenic variation in growth (Hérault *et al.* 2011), growth differences in the natural habitat was also examined separately for each 20 cm diameter class. This was preferred to the relative growth rate to account for the nonlinear relationship between growth and size (Hérault *et al.* 2011).

2.6 Life-history traits

More general traits such as wood density, light requirement and seed mass were examined. Basic wood density was extracted from the Global Wood Density Database (Zanne *et al.* 2009) and also measured on branch samples (oven dry mass/green volume, volume was estimated assuming a cylindrical form). Light requirement and seed mass were derived from observations and samples collected in the natural habitat of the species.

To quantify the light requirement at juvenile and mature stages, crown exposure (CE) to light was visually estimated for *E. ivorense* (n = 189 trees covering the species diameter range) and *E. suaveolens* (n = 295), following Poorter and Kitajima (2007). The CE varies between 1, for understory trees that do not receive any direct light, and 5 for emergent trees fully exposed to light. The CE was related to tree diameter using a multinomial logistic regression (Sheil *et al.* 2006), and the CE at a diameter of 10 cm (CEI_{juv}) was estimated.

Seed mass was measured on dry seeds collected on well-spaced mother trees (27 seeds from four mother trees for *E. ivorense* and 21 seeds from four trees for *E. suaveolens*). The seeds were dried at 80°C for at least 48h following the standardized protocol proposed by Cornelissen *et al.* (2003).

3 Results

3.1 Hydraulic traits

The wet forest species, *E. ivorense*, was less resistant to drought-induced embolism, with an average AE50 (± SD), the 50% embolism-related acoustic emission, of -1.93 ± 0.03 MPa (**Figure 4.3a**). The moist forest species *E. suaveolens* showed half the value of AE50 (−3.88 ± 0.70 MPa, **Figure 4.3a**). Branches were completely desiccated within 1.88 ± 0.02 days for *E. ivorense* and 3.73 ± 0.56 days for *E. suaveolens*.

Branches had an average (± SD) initial volumetric water content (VWC) of 861 ± 65 kg/m³ for *E. ivorense* and 680 ± 20 kg/m³ for *E. suaveolens* (**Figure 4.3b**). As the dehydration progressed, the wet forest species, *E. ivorense*, was characterized by slightly lower elastic hydraulic capacitance (C_{el}, capacitance of Phase I) compared to the moist forest species, *E. suaveolens* (respectively 68 ± 22 vs 94 ± 32 kg/m³/MPa, r^2=0.99, **Figure 4.3b**). In contrast, the inelastic capacitance (C_{inel}, capacitance of Phase II) was four times higher for *E. ivorense* than for *E. suaveolens* (138 ± 34 *vs* 35 ± 14 kg/m³/MPa, r^2=0.99, **Figure 4.3b**). The overall capacitance was higher for *E. ivorense* (108.72 ± 1.68 kg/m³/MPa, r^2 = 0.98), than for *E. suaveolens* (51.48 ± 1.25 kg/m³.MPa, r^2 = 0.94).

The amount of water released by the wet forest species *E. ivorense* is lower than that of the moist forest species, *E. suaveolens*. For *E. ivorense* VWC decreased by 8% during the elastic phase and in total by 20% at the end of the inelastic phase (146 kg/m³) while for *E. suaveolens*, VWC decreased by 21% during the elastic phase and in total by 38% at the end of the inelastic phase (246 kg/m³, **Figure 4.3b**).

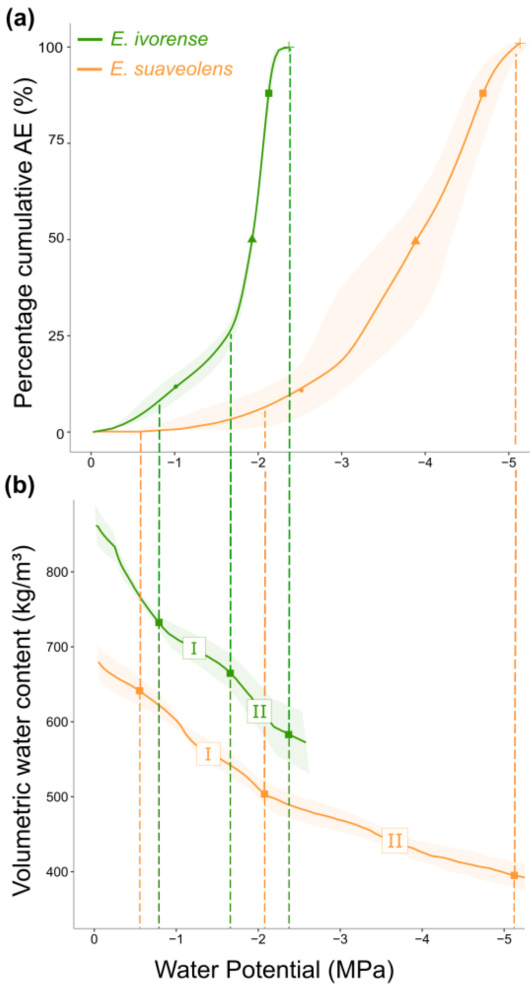


Figure 4.3 Hydraulic traits. Acoustic vulnerability curves (a) and desorption curves (b) for the wet forest species *Erythrophleum ivorense* (green) and the moist forest species *E. suaveolens* (orange). Curves were computed on three individuals per species collected in their natural habitat. The average acoustic vulnerability curves with standard error margins (±SE) was obtained by plotting cumulative AE values against xylem water potential. The vulnerability thresholds AE$_{12}$ (circle), AE$_{50}$ (triangle), AE$_{88}$ (square) and AE$_{100}$ (cross) are indicated as well. Desorption curves with standard error margins (±SE) were obtained by plotting average volumetric water content against xylem water potential during the bench dehydration experiment. Phases I and II are delimited by vertical lines and the slopes within these phases represent elastic (C$_{el}$) and inelastic (C$_{inel}$) hydraulic capacitance, respectively.

3.2 Wood traits

Given the strong differences in tree hydraulics between the two sister species (**Figure 4.3**), we further examined differences in wood anatomical traits, especially those related to hydraulic conduits (**Table 4.1**). We identified some slight differences in wood traits, particularly in vessel-associated traits. In the natural habitat, *E. ivorense* showed a larger tangential vessel diameter, lower vessel density and vessel wall reinforcement, and larger diameter of intervessel pits compared to *E. suaveolens* **(Figure 4.4a,b**, **Table 4.1**). Other wood traits, including vessel grouping index, fiber wall thickness and proportion of vessel, fibre, parenchyma, did not differ between the species (**Table 4.1**). Differences in wood traits observed in the natural habitat were maintained in the common garden experiment (**Figure 4.4c**, **Figure 4.1a**, **Table 4.1**), arguing for a genotypic origin rather than environmental plasticity. Overall, vessel diameter and the proportion of vessel lumen increased with distance to the pith for *E. ivorense* and *E. suaveolens* in both natural habitats and in the common garden experiment (**Figure 4.4a,c**, **Table 4.1**).

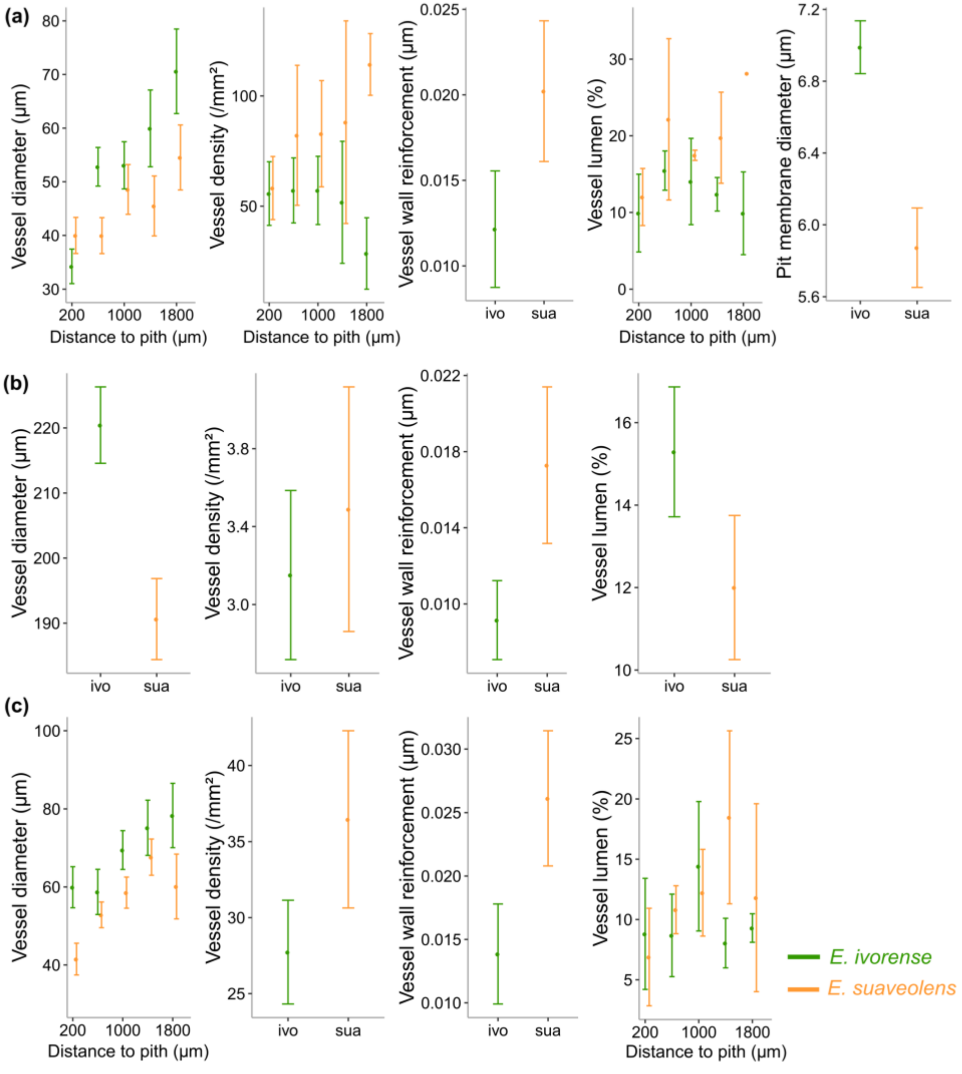


Figure 4.4 Wood traits. Average of vessel diameter, vessel density, vessel wall reinforcement, percentage of vessel lumen and intervessel pit diameter (only for branches collected in the natural habitat) and 95% confidence intervals for branches (n=5) and stem (n=5) collected in the natural habitat (respectively a and b) and for branch samples (n=5) collected in a common garden experiment (c) for the wet forest species *Erythrophleum ivorense* (green) and the moist forest species *E. suaveolens* (orange).

Table 4.1 Fixed parameter estimates, standard error (SE), *P*-values and variance of the residuals ($\sigma\ \varepsilon_{i|sp}$) for the best linear mixed model for testing differences in wood traits between *Erythrophleum ivorense* (ivo) and *E. suaveolens* (sua).

	Wood traits	**Parameter estimate ± SE**		***P*-value**	**$\sigma\ \varepsilon_{i\|sp}$**
Branch in natural habitats	Vessel diameter (µm)	a =	34.96 ± 2.73	<.0001	16.32
		b_{ivo} =	7.07 ± 0.88	<.0001	
		b_{sua} =	4.32 ± 0.81	<.0001	
	Vessel density (/mm^2)	a =	56.51 ± 8.27	<.0001	23.42
		b_{ivo} =	-1.25 ± 2.96	0.57	
		b_{sua} =	7.89 ± 3.48	<.05	
	Vessel grouping index	a =	1.7 ± 0.08	<.0001	0.65
	Vessel wall reinforcement (µm)	a_{ivo} =	0.01 ± 0.002	<.0001	0.17
		a_{ua} =	0.02 ± 0.002	<.001	
	Fibre wall thickness (µm)	a =	5.33 ± 0.21	<.0001	1.06
	Vessel lumen (%)	a =	10.71 ± 2.33	<.0001	5.68
		b_{ivo} =	0.74 ± 0.78	0.35	
		b_{sua} =	3.84 ± 0.10	< .001	
	Axial parenchyma (%)	a =	31.67 ± 4.78	<.0001	12.2
	Radial parenchyma (%)	a_{ivo} =	12.00 ± 1.54	<.0001	4.27
		a_{sua} =	15.59 ± 1.56	0.055	
		b =	-1.35 ± 0.49	< .01	
	Fibre (%)	a_{ivo} =	50.01 ± 6.09	<.0001	14.18
		a_{sua} =	52.46 ± 7.16	0.74	
		b =	-3.68 ± 1.69	< .05	
	Pit membrane diameter (µm)	a_{ivo} =	7.03 ± 0.20	<.001	0.92
		a_{sua} =	5.87 ± 0.31	<.01	
Stem in natural habitats	Vessel diameter (µm)	a_{ivo} =	229.50 ± 10.44	<.001	54.05
		a_{sua} =	190.93 ± 17.35	<.05	
	Vessel density (/mm)	a =	3.28 ± 0.25	<.0001	0.87
	Vessel grouping index	a =	1.45 ± 0.07	<.0001	0.17
	Vessel wall reinforcement (µm)	a_{ivo} =	0.009 ± 0.002	<.0001	0.009
		a_{sua} =	0.017 ± 0.003	<.05	
	Fibre wall thickness (µm)	a =	9.16 ± 0.40	<.0001	1.95
	Vessel lumen (%)	a =	13.97 ± 1.21	<.0001	1.77
	Axial parenchyma (%)	a =	37.75 ± 2.29	<.0001	6.41
	Radial parenchyma (%)	a =	8.63 ± 1.60	<.0001	3.36
	Fibre (%)	a =	40.05 ± 1.66	<.0001	11.71

The model selection was based on the Akaike's information criterion. For stem, model tested estimated wood trait (*WT*) of the individuals (*i*) belonging to each species (*sp*), with a random intercept (α): $WT_{i,sp} = a_{sp} + \alpha_{i,sp} + \varepsilon_{i,sp}$. For branch, the effect of the distance to the pith (*dist*) and a random slope (β) have been added in order to consider radial variation in wood anatomy: $WT_{i,sp} = a_{sp} + b_{sp} \times \text{dist} + \alpha_{i,sp} + \beta_{i,sp} \times \text{dist} + \varepsilon_{i,sp}$; with a_{sp} and b_{sp} as fixed parameters, $\alpha_{i,sp}$ and $\beta_{i,sp}$ as random parameters, and $\varepsilon_{i,sp}$ as the random error.

Table 4.1 Fixed parameter estimates, standard error (SE), *P*-values and variance of the residuals ($\sigma\ \varepsilon_{i|sp}$) for the best linear mixed model for testing differences in wood traits between *Erythrophleum ivorense* (ivo) and *E. suaveolens* (sua).

	Wood traits	**Parameter estimate ± SE**		***P*-value**	**$\sigma\ \varepsilon_{i|sp}$**
Branch in common garden	Vessel diameter (µm)	a_{ivo} =	49.15 ± 3.50	<.0001	14.5
		a_{sua} =	38.71 ± 4.21	<.05	
		b =	6.35 ± 0.55	<.0001	
	Vessel density (/mm^2)	a_{ivo} =	27.83 ± 2.07	<.0001	13.66
		a_{ivo} =	40.57 ± 6.89	0.091	
	Vessel grouping index	a =	1.55± 0.09	<.0001	0.92
	Vessel wall reinforcement (µm)	a_{ivo} =	0.014 ± 0.003	<.0001	0.011
		a_{ivo} =	0.026 ± 0.005	<.05	
	Fibre wall thickness (µm)	a =	5.07± 0.26	<.0001	0.92
	Vessel lumen (%)	a =	7.75 ± 1.67	<.0001	4.66
		b_{ivo} =	0.55 ± 0.56	0.34	
		b_{sua} =	1.83 ± 0.62	< .01	
	Axial parenchyma (%)	a=	17.11 ± 2.10	<.0001	8.53
	Radial parenchyma (%)	a =	20.39 ± 2.87	<.0001	11.71
	Fibre (%)	a =	46.34 ± 2.91	<.0001	15.43

3.3 Growth

The wet forest species *E. ivorense* had a faster inherent growth than *E. suaveolens* (**Figure 4.5a, b, c**). For all diameters combined and in their natural habitat, the average diameter increment of *E. ivorense* was significantly higher than that of *E. suaveolens* (0.56 ± 0.36 cm/yr *vs* 0.40 ± 0.37 cm/yr, one-way ANOVA F-value = 6.74, P-value < 0.05, Figure 5A). Although *E. ivorense* was under-represented in diameter classes lower than 40 cm and higher than 80 cm, the faster growth of *E. ivorense* was mainly maintained when size/ontogeny was taken into account (**Figure 4.5b**).

In the common garden experiment, the growth difference between the two species was maintained and strengthened (2.59 ± 0.92 cm/yr for *E. ivorense* vs 1.63 ± 0.64 cm/yr for *E. suaveolens*, one-way ANOVA F-value = 78.62, P-value < 0.001, **Figure 4.5c**). Thus, juvenile trees of *E. suaveolens* did not exhibit any home advantage in terms of growth. The two species grew faster in the common garden experiment, probably due to the absence of competitors and higher light availability in the plantation.

3.4 Life-history traits

Wood density of the wet forest species *E. ivorense* tended to be lower than that of the moist forest species, *E. suaveolens* (**Table 4.2**). The, Crown Exposure Index, the CEI_{juv}, which approximates light requirements at juvenile stage, was higher for the wet forest species *E. ivorense* than for the moist forest species *E. suaveolens* (2.14 *vs* 1.57) and reflected the establishment of *E. ivorense* in higher light conditions. Finally, the average (± SD) seed mass of *E. ivorense* was half that of *E. suaveolens* (1.46 ± 0.26 g *vs* 3.02 ± 0.26 g).

Table 4.2 Light requirement and life-history traits for the wet forest species *Erythrophleum ivorense* and for the moist forest species *E. suaveolens* (CEI_{juv} correspond to the crown exposure index at 10 cm).

	E. ivorense	***E. suaveolens***
CEI_{juv}	2.14	1.57
Seed mass (g)	1.46 ± 0.26	3.02 ± 0.26
Wood density (g/cm^3) from the Global Wood Density Database (Zanne *et al.* 2009)	0.77 ± 0.06	0.82 ± 0.03
In situ branch wood density (g/cm^3)	0.49 ± 0.04	0.58 ± 0.05
Common garden branch wood density (g/cm^3)	0.50 ± 0.04	0.49 ± 0.03

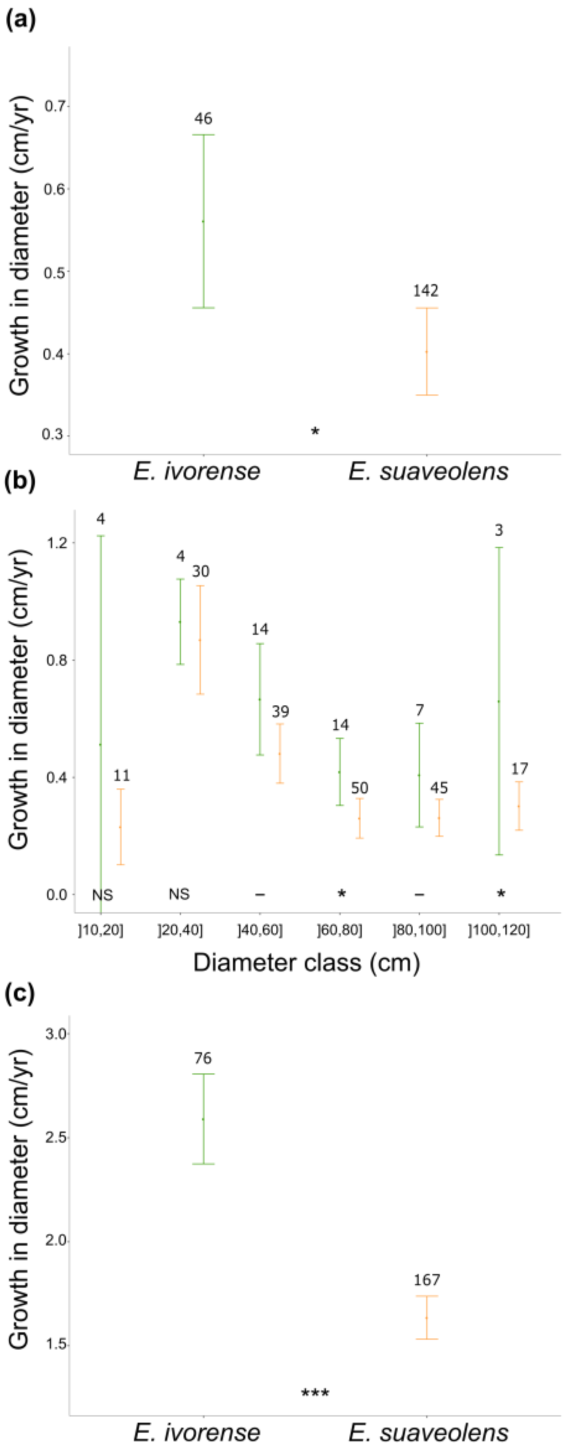


Figure 4.5 Average growth and 95% confidence intervals of the wet forest species *Erythrophleum ivorense* (green) and of the moist forest species *E. suaveolens* (orange) in the natural habitat (a), in natural habitat by diameter classes (b) and in the common garden experiment (c). Significance of the one-way ANOVA tests is given, with NS: *P-value*>0.1, -: *P-value*<0.1, *: *P-value*<0.05, and ***: *P-value*<0.001. Number of individuals is given above each line range.

4 Discussion

Tropical tree species distribution along rainfall gradients, and underlying drought response strategies, hydraulics, and wood anatomical traits have previously been examined (Engelbrecht *et al.* 2007, Poorter & Markesteijn 2008, Maharjan *et al.* 2011, Sterck *et al.* 2014, Gaviria & Engelbrecht 2015, Gaviria *et al.* 2017), but not necessarily on closely related species (but see Pfautsch *et al.* 2016 for Eucalyptus). In this study, we examined how tree species evolved on a rainfall gradient with an integrated eco-physio-morphological approach. Our two species, *E. ivorense* and *E. suaveolens*, broadly share the same general wood anatomical features (Inside Wood 2004) and are hard to distinguish in the field, though genetic studies showed contrasted distributions. Here, we identified some slight differences in wood traits that resulted in strong differences in tree hydraulics, growth, and overall species distribution. The conserved between-species differences in wood trait and growth in the natural habitat and in the common garden argue for a genotypic origin rather than environmental plasticity as discussed by Pfautsch *et al.* (2016). We cautiously interpret these differences as reflecting a long-term adaptation to drought.

As expected, the wet forest species, *E. ivorense,* had lower resistance to embolism than the moist forest species, *E. suaveolens*. The tension at which the xylem experiences 50% loss of conductivity (ψ_{50} or the equivalent AE_{50} in the acoustic method) is usually used as a benchmark for species comparison (Anderegg 2015). For the wet forest species *E. ivorense*, the average AE_{50} value of –1.9 ± 0.1 MPa reported here is similar to that reported by Markesteijn *et al.* (2011) for pioneer saplings (–1.8 ± 0.4 MPa), in line with its high light-requirement. The moist forest species, *E. suaveolens*, was less vulnerable, with a lower AE_{50} of −3.9 ± 0.5 MPa. Following Choat *et al.* (2012), such a value indicates low vulnerability to drought-induced embolism, with only 10% of the tropical tree species sampled worldwide showing lower vulnerability. Resistance to embolism in the *Erythrophleum* genus appeared to be mainly controlled by differences in vessel characteristics. The higher resistance to embolism of the moist forest species, *E. suaveolens*, was associated with shallower intervessel-pit chambers and smaller vessel diameters, which have the benefit of minimizing embolism risk (Lens *et al.* 2011, Li *et al.* 2016), but reduce hydraulic conductivity (Wheeler *et al.* 2005, Choat *et al.* 2006).

In addition to the relatively classical drought-induced embolism, we also examined hydraulic traits that are often-neglected: wood volumetric water content and hydraulic capacitance (Vergeynst, Dierick, *et al.* 2015, Epila, Maes, *et al.* 2017). These traits, which are involved in desiccation delay strategies, determine the capacity of a species to buffer increases in xylem tension (Sperry *et al.* 2008, Anderegg & Meinzer 2015) and to limit embolism formation (Phillips *et al.* 2004). As previously reported for tropical trees, we found that the species with the lowest resistance to embolism and the lowest wood density, *i.e.* the wet forest species *E. ivorense*, also showed the highest wood volumetric water content (Borchert 1994) and the highest overall hydraulic capacitance (Borchert 1998, Meinzer *et al.* 2003, Borchert & Pockman 2005, Mcculloh Katherine A. *et al.* 2013, Oliva Carrasco *et al.* 2015). Notwithstanding these points, during desiccation, the amount of water released by the moist forest species, *E. suaveolens*, is higher (246 kg/m^3) than that of the wet forest species, *E. ivorense* (146 kg/m^3). Associated with strong embolism-resistant xylem conduits, this contributed to the delay for complete dehydration (four days) in *E. suaveolens* while it took less than two days for *E. ivorense*. Undoubtedly, these two hydraulic strategies confer an adaptive value under drought episodes of different intensity and/or duration. During short dry periods, the high hydraulic capacitance of *E. ivorense* allows avoiding a large percentage of embolism formation in the xylem (Oliva Carrasco *et al.* 2015). During intense and longer drought periods, the strong embolism resistance of *E. suaveolens*, associated with a continuous internal water supply of the xylem, contributes to a higher fitness (Sperry *et al.* 2008).

The computation of hydraulic capacitance for the elastic and the inelastic phases, allowed us to investigate the fine-scale mechanisms of internal water transfer (Vergeynst, Dierick, *et al.* 2015) and was complemented by detailed analysis of associated wood traits. The elastic phase (and the related capacitance, C_{el}) occurs when water is released from the elastic shrinkage of living cells. In contrast, the inelastic phase (and C_{inel}) occurs when embolism is strong and water is released from embolized conduits into the still functional ones. The wet forest species, *E. ivorense*, was characterized by a lower C_{el} compared to the moist forest species *E. suaveolens* (respectively 68 ± 22 *vs* 94 ± 32 kg/m^3/MPa), and a four times higher C_{inel} value (138 ± 34 *vs* 35 ± 14 kg/m^3/MPa). During the elastic phase, the role of the parenchyma in refilling conduits has mainly been invoked (Borchert & Pockman 2005, Brodersen & McElrone 2013, Morris & Jansen 2016). Contrary to expectation, we did not find a positive link between C_{el} and the proportion of axial and/or radial parenchyma. But it is possible that the water stored in other tissues, such as bark and pith, contributes to C_{el} (Wolfe & Kursar 2015). The higher C_{inel} for the wet forest species, *E. ivorense*, might be attributed to the larger vessels compared to those of the moist forest species. Indeed, because the vessels are inherently larger, the amount of water released from one embolized vessel is expected to be higher. At the same time, the higher vessel density of the moist forest species, *E. suaveolens*, enables the embolism of a higher portion of conduits to safeguard the still functional ones. The production of many small vessels could be advantageous in drier environments, because a large proportion of small vessels can serve as a water reservoir to mitigate drought-induced xylem tension, in addition to the greater resistance to embolism (Zanne *et al.* 2014).

When examining more classical functional traits for tropical tree species, the wet forest species, *E. ivorense*, showed characteristics of a fast growing species, with a high light demand (high CEI_{juv}) and small seeds (Westoby 1998, Myers & Kitajima 2007). In contrast, the moist forest species, *E. suaveolens*, showed traits indicative of a better adaptation to stressful understory conditions at the juvenile stage. The light demand of the wet forest species, *E. ivorense*, was similar to values reported by

Poorter & Kitajima (2007) for tropical pioneers while that of the moist forest species, *E. suaveolens*, was indicative of partial shade tolerance (Sheil *et al.* 2006). Seed mass is an important component of the life-history strategy (Westoby 1998). The seed mass of the wet forest species was half that of the moist forest species. Fast growing species tend to have smaller seeds, while species with larger seeds survive better under drought and shaded conditions (Westoby 1998, Moles & Westoby 2006). These results point towards a coordinated drought and shade tolerance of *E. suaveolens*, and do not support for a trade-off between shade and drought tolerance as proposed by Brenes-Arguedas *et al.* (2009) for 24 tropical tree species across the Isthmus of Panama.

Finally, the faster growth of wet forest species has previously been observed in Panama (Brenes-Arguedas *et al.* 2009, Gaviria & Engelbrecht 2015, Gaviria *et al.* 2017) and in Bolivia (Markesteijn & Poorter 2009). Here, the fast growth of the wet forest species was related to wood traits allowing a high hydraulic conductivity (Tyree *et al.* 1994, Sperry *et al.* 2008, Anderegg & Meinzer 2015) which could in turn maintain high transpiration and photosynthetic rates (Santiago *et al.* 2004). These wood traits, however, confer sensitivity to embolism, and overall drought sensitivity (Tyree *et al.* 1994, Markesteijn, Poorter, Bongers, *et al.* 2011). In contrast, the slow growth rate of the drought-tolerant moist forest species, *E. suaveolens*, has been interpreted as the cost resulting from stress adaptation (Smith & Huston 1990). The specialization to drier environments promotes wood traits that result in lower vulnerability to drought-induced embolism at the cost of reduced water transport efficiency (Sperry *et al.* 2008) and lower growth rate (Polley *et al.* 2002, Gaviria & Engelbrecht 2015).

Our results confirm a trade-off between drought tolerance and growth, controlled by subtle adaptations in wood traits, as a key mechanism leading to the niche partitioning between the two *Erythrophleum* species. The low drought tolerance of the wet forest species, *E. ivorense*, likely explains its exclusion from the moist and seasonal forests (Currie *et al.* 2004). In contrast, the high drought tolerance of the moist forest species, *E. suaveolens*, due to the combined action of a low vulnerability to embolism and a desiccation delay-strategy, seems to be associated with a low growth rate and certainly with a competitive exclusion from wet forests (Markesteijn & Poorter 2009, Gaviria & Engelbrecht 2015). The importance of this trade-off in the diversification of the African tree flora remains to be tested and an integrated eco-physio-morphological approach linking wood anatomy, hydraulics, growth and distribution, as developed here could be the way forward.

5

The functional understanding of niche evolution

Part II: Stomatal control and stem photosynthesis

1 Preamble

For the two forest species of *Erythrophleum* in Africa, evidence has been accumulated on the association between niche evolution and changes in xylem resistance to embolism and desiccation delay strategies, controlled by subtle adaptation in wood anatomical traits (**Chapter 4**). In addition to these hydraulic traits, other mechanisms prevent xylem from reaching critical water potential and prolong survival during drought. Among them, we explored the regulation of gas exchanges at the leaf level and the possibility to get carbon from photosynthetic stems (Meinzer *et al.* 2008, Choat *et al.* 2012, Santiago *et al.* 2016).

In this chapter, we present the unpublished results of a controlled experiment designed to examine the effects of drought on the physiology, wilting and mortality of 1-year old seedlings of the two sister species: *E. ivorense* and *E. suaveolens*. In order to locate these two species along the continuum of iso- to anisohydric behaviors, we measured leaf gas exchanges and plant water status of control (well-watered) and drought-stressed (water-withheld) seedlings over time. On one side of the continuum, isohydric plants are expected to close their stomata early in response to drought, thereby maintaining constant leaf water potential and avoiding severe hydraulic failure. At the other side, anisohydric plants exhibit lower stomatal responsiveness and maintain high transpiration rates and high productivity under drought conditions (McDowell *et al.* 2008). To further examine the contribution of woody tissue photosynthesis to drought stress tolerance, half of the drought-stressed seedlings were subjected to a stem light-exclusion treatment to prevent bark and woody tissue photosynthesis.

This ecophysiological study has not been published yet, but RNA material was collected on the seedlings, before the water-withheld, and 2 and 6 weeks after, to analyze the transcriptomes. The genetic study has been published in *Gene* in a paper entitled "*Comparative analysis of two sister* Erythrophleum *species (Leguminosae) reveal contrasting transcriptome-wide responses to early drought stress*" (Neji *et al.* 2019).

2 Methods

2.1 Plant material and experimental design

The experiment was conducted in the Laboratory for Plant Ecology of Ghent University, in a green-house, on 1-year old potted *E. ivorense* and *E. suaveolens* seedlings, in winter, from November 2016 through February 2017 (**Figure 5.1**).

Figure 5.1 Controlled experiment on 1-year old potted *E. ivorense* and *E. suaveolens* seedlings (a) and leaf gas exchanges measurements with the Licor system (b, Li-6400, Licor, Inc., Lincoln, NE, USA)

We obtained seeds from the species natural habitat (**Chapter 3** and **4**): *Erythrophleum ivorense* seeds were from Ma'an (south-west Cameroon) and *E. suaveolens* seeds from Mindourou (south-east Cameroon). Seeds were germinated and seedlings nursery-grown in 2.12L containers during one year. Until the experiment, all seedlings were irrigated 3-4 times per week.

For each species, 10 seedlings were randomly assigned to one of two experimental groups (**Table 5.1**). The first group consisted of 5 seedlings per species for which leaf gas exchanges were measured throughout the experiment. The second group consisted of 5 seedlings per species for which leaf water potential (Ψ) was measured. Within each group, one seedling was maintained under well-watered conditions throughout the experiment (control; C), two seedlings were assigned to a drought treatment (without watering; D) and two seedlings were assigned to the same drought treatment and their shoots were completely covered to prevent stem photosynthesis (hereafter calls "drought and packed" treatment; DP). Throughout the experiment, soil water content (SWC, measured as percentage saturation) was measured on each plant using a portable soil water content measurement system (SM150T Soil Moisture Sensor, Delta-T Devices, United Kingdom). Growth in diameter was measured on control seedlings.

Table 5.1 Experimental design. For each species, number of individuals per treatment (control: C, drought: D, drought and packed: DP) and experimental group of measures.

		E. ivorense			*E. suaveolens*			
Experimental group	Measures	C	D	DP	C	D	DP	Total
Group 1	Gas exchange g_s, E, A	1	2	2	1	2	2	10
Group 2	Plant water status Ψ	1	2	2	1	2	2	10
All seedlings (Group 1 & 2)	Wilted stage Mortality SWC	2	4	4	2	4	4	20

2.2 Wilting stage and mortality

Before the death of seedlings, the effect of water withheld can be observed with the wilting stage. Here, we adapted the wilting stages (WS) from the study of Tyree *et al.* (2002) on *Licania platypus* as follows: (0) No sign of wilting; (1) Slightly wilted: leaves green but leaflets angled slightly towards the ground compared to controls; (2) Wilted: leaves green with some leaflets (< 20 %) with angles near 45° and leaf blades have begun to fold (curl) inward parallel to midrib; (3) Severely-wilted: leaves green, most leaflets angles near 90° from horizontal and around 50% of leaflets with extensive curling; (4) Nearly-dead: the majority of leaflets have angles near 90° with extensive curling and loss of elasticity; (5) Dead: all the leaflets are curl and dry. The WS was visually assessed for all seedlings (group 1 & 2) every week (**Table 5.1)**.

Seedlings were monitored until death. To model mortality, we estimated the probability of death of one seedling over time using the nonparametric Kaplan–Meier method. Within each species, the mortality curves were compared for each treatment (D and DP) with a log-rank test. Since there was no difference, we pooled the D and DP seedlings to test for between-species differences in mortality. The null hypothesis of the log-rank test is that mortality curves of two populations do not differ. The mortality analysis were done with the *survival* package (Therneau & Grambsch 2013) in the open source R software (R Core Team 2016).

2.3 Leaf gas exchanges and plant water status

In order to explore the ability of stomata to control transpiration, leaf gas exchanges were measured using a portable open gas exchange system (Li-6400, Licor, Inc., Lincoln, NE, USA) on one leaflet per plant during mid-day (10:00-16:00h). Light-saturated gas exchange rates were measured on the same mature leaflet during the experiment with a standard leaf chamber equipped with a blue-red light source at PPFD of 750 µmol/m²/s², which corresponds to the light intensity maximizing photosynthesis according to light response curves built on three seedlings per species before the experiment (results not shown). Air temperature inside the chamber was maintained between 23 and 25°C. Leaf area was used to calculate stomatal conductance (g_s), transpiration rate (E) and net photosynthetic rate (A). The vapor-pressure deficit based on leaf temperature (Vpd) and the concentration of CO_2 in the Licor chamber were used to identify their influence on leaf gas flux. Daytime leaf water potential (Ψ) was measured using a thermocouple psychrometer (sample chambers type C52; Wescor lnc, Logan, Utah, USA).

For each species, the effect of SWC, Vpd and CO_2 concentration on leaf gas flux were assessed by Pearson correlation tests and graphically represented. Then, to locate the two species along the continuum of iso- to anisohydric behaviors, the relationships between mean leaf water potential (Ψ) and mean conductance (g_s) calculated for each census were also assessed by Pearson correlation tests and graphically represented.

3 Results

3.1 Experimental conditions

To verify the intensity of the drought stress imposed to the seedlings, we monitored the Soil Water Content (SWC) over time along the experiment (**Figure 5.2a)**. As expected, the SWC of control plants was stable, with an average of 54.51% (± 18%) thorough the experiment. For the seedlings under the drought treatments (D and DP), the SWC decreased exponentially after the cessation of watering. After 70 days, the SWC felled to 0.81 ± 0.65% for *E. ivorense* and 2.90 ± 3.55% for *E. suaveolens*. All seedlings under drought treatments (D and DP) died by the end of the experiment, except one *E. suaveolens* seedling assigned to the DP treatment. Vapour pressure deficit (Vpd) and CO_2 concentration varied over time, with no obvious trend (**Figure 5.2b**). CO_2 concentration decreased with SWC (r-Pearson=0.50, *p-value*<0.001) and Vpd (r-Pearson=0.51, *p-value*<0.001). We found no correlation between SWC and Vpd (r-Pearson=0.03, *p-value*=0.84). Temperature and light intensity were stable along the experiment. In average (±SE), the temperature was maintain around 25.60°C (± 0.003) and PAR at midday was low, around 80 µmol/m²/s² (± 1.72). During the experiment, the growth in diameter of control seedlings was 0.35 mm (1.73 mm/yr) for *E. ivorense* and 0.29 mm (1.49mm/yr) for *E. suaveolens* seedlings. These low growth rate may reflect the poor light conditions inside the greenhouse.

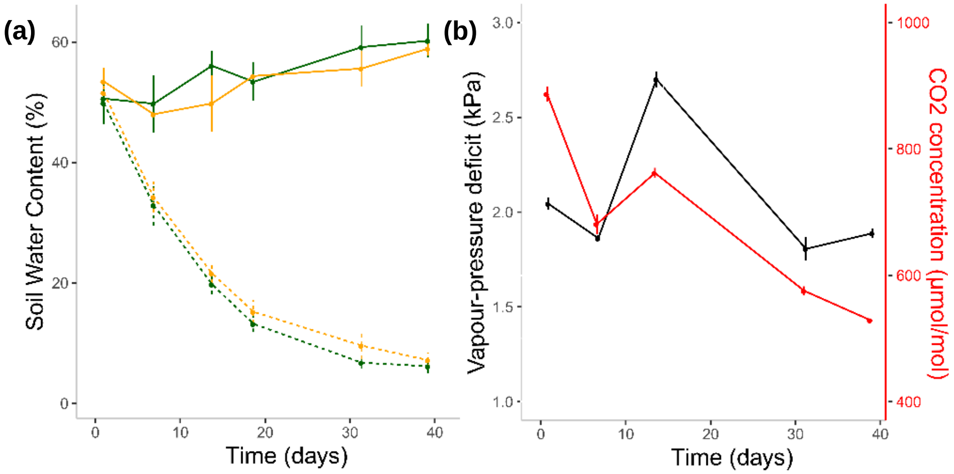


Figure 5.2 (a) Average soil water content (± SE, % of saturation) over time for the control (solid lines) and drought-stressed seedlings (dashed-lines) for the two species *E. ivorense* (in green) and *E. suaveolens* (in orange). (b) Vapour pressure deficit (Vpd) and CO_2 concentration over time.

3.2 Wilting stage and mortality

The effect of drought on seedlings differed between species when considering wilting and mortality. First signs of wilting appeared quickly on the drought stressed seedlings of *E. suaveolens* (after 14 days (median)). Then, the seedlings followed a slow continuum of wilting stages as the dehydration progress **(Figure 5.3a)**. For *E. ivorense*, first signs of wilting were delayed (40 days). However, the seedlings quickly reached catastrophic wilting stages, quickly followed by death (**Figure 5.3a**). Seedlings of *E. suaveolens* survived significantly longer under drought than that of *E. ivorense* (for D and DP treatments pooled the log-rank p-value of the survival model was 0.03, **Figure 5.3b**). Seedlings of *E. suaveolens* survived 72 days (median) against 50 days for that of *E. ivorense*. For each species, no clear differences were observed between the two treatments (D and DP) when considering wilting (visual observation) and mortality (log-rank *p-value* = 0.58 for *E. ivorense* and 0.27 for *E. suaveolens*).

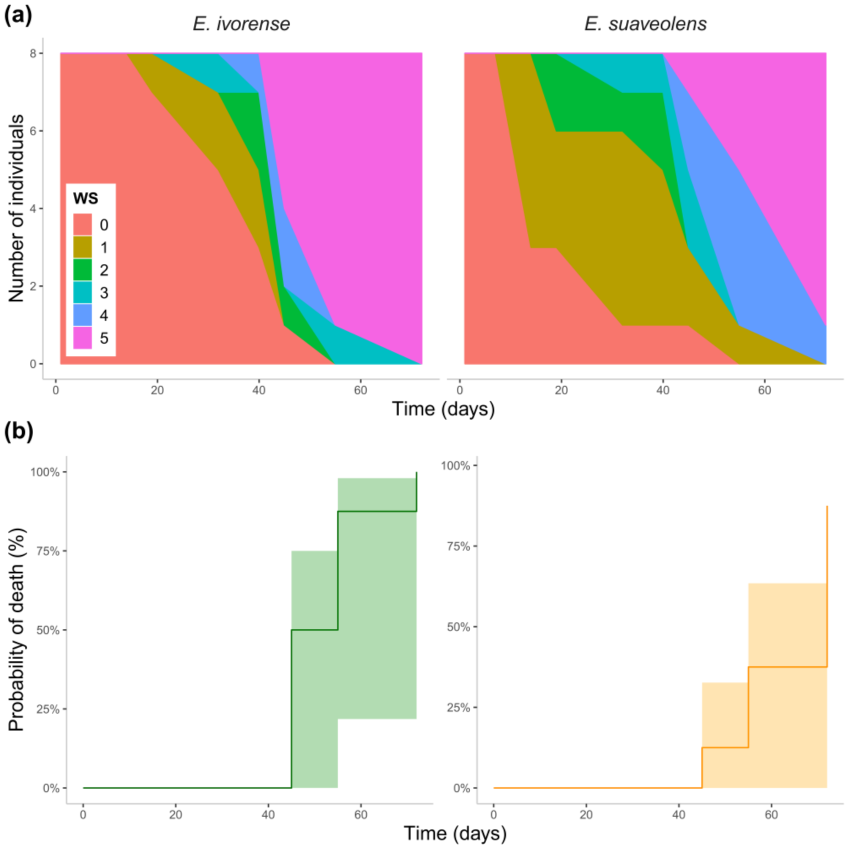


Figure 5.3 (a) Wilting stages (WS) over time (b) and mortality curves (green line: *E. ivorense*, orange line: *E. suaveolens*) of the two species *E. ivorense* and *E. suaveolens* subjected to drought (D and DP treatments pooled).

3.3 Leaf gas exchanges and plant water status

Using the huge body of ecophysiological measurements made throughout the experiment (every week from the cessation of plant watering and up to 10 weeks until most seedlings died), we found that seedlings of *E. ivorense* and *E. suaveolens* had contrasting stomatal responses to soil dehydration. Compared to *E. ivorense* ones, seedlings of *E. suaveolens* had higher conductance, transpiration and photosynthesis in well-watered conditions. When soil dehydration progress, conductance, transpiration and photosynthesis decreased, providing evidence for stomatal control. In contrast, seedlings of *E. ivorense* maintained constant conductance, transpiration and photosynthesis (**Figure 5.4a, b, c**). For the two species, conductance and transpiration increased linearly with vapor-pressure deficit (**Figure 5.4d, e**), but did not clearly respond to CO_2 (**Figure 5.4g, h, i**).

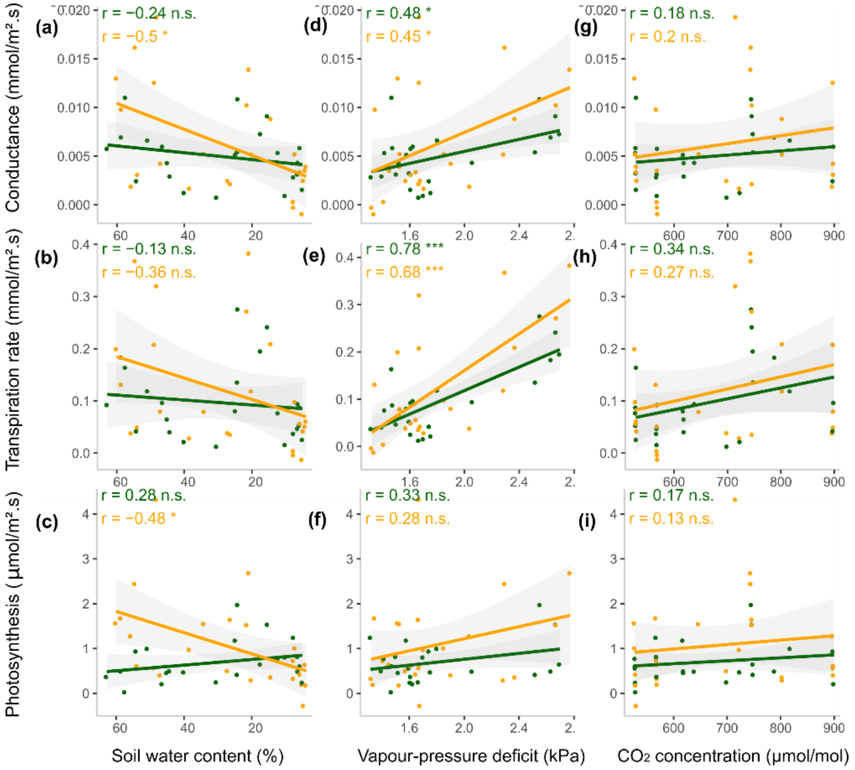


Figure 5.4 Effect of soil water content (a, b, c), vapor-pressure deficit (d, e, f) and CO_2 concentration (g, h, i) on conductance, transpiration rate and photosynthesis for seedlings of *E. ivorense* (green) and *E. suaveolens* (orange). Pearson correlation coefficients and significativity for each species (n.s: *P-value*>0.1, -: *P-value*<0.1, *: *P-value*<0.05, and ***: *P-value*<0.001) were shown on graphs and linear smoothing (±se) were used to highlight trends.

For *E. suaveolens* seedlings, the decrease in conductance during dehydration allowed to mitigate decline in leaf water potential (**Figure 5.5**), which indicates an isohydric behaviour. In contrast, for *E. ivorense* seedlings, the maintenance of transpiration and photosynthesis leaded to drop in water potential, indicative of a more anisohydric behaviour (**Figure 5.5**).

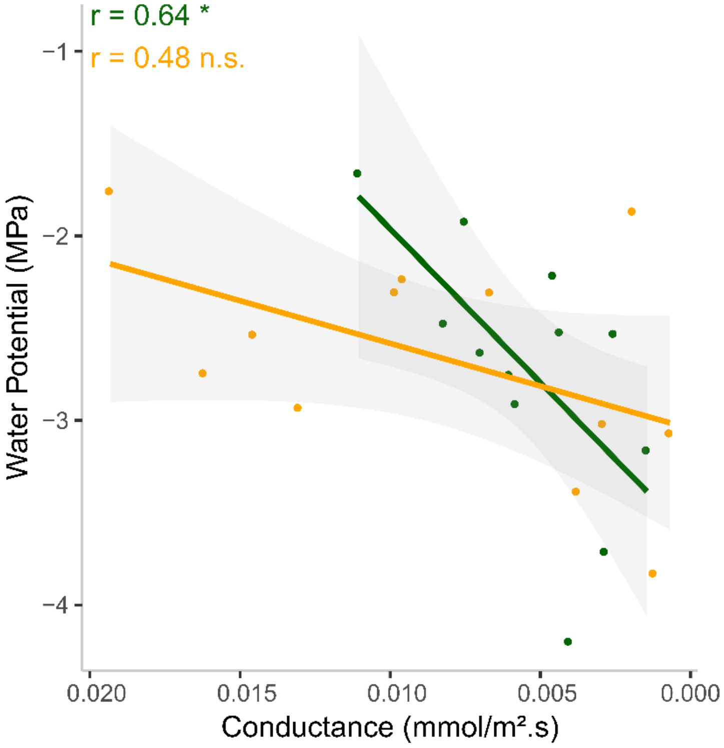


Figure 5.5 Mean water potential over mean conductance calculated at each census for *E. ivorense* seedlings (green) and *E. suaveolens* seedlings (orange). For each species, Pearson correlation coefficients and significativity (n.s: P-value>0.1, -: P-value<0.1, *: P-value<0.05, and ***: P-value<0.001) were shown on graphs and linear smoothing (±se) were used to highlight trends.

4 Discussion

Our experiment revealed that 1-year seedlings of *E. suaveolens* and *E. ivorense* showed contrasting responses to drought, in terms of gas exchanges, reflecting adaptation to their native environmental conditions. During drought, seedlings of *E. suaveolens* had a more stringent stomatal control, reducing transpiration to mitigate decline in leaf water potential. This more isohydric behavior ensure that water demand from the leaves does not exceed the supply capacity of the hydraulic system, limiting embolism and plant desiccation (Sperry 2004, McDowell *et al.* 2008). In contrast, seedlings of *E. ivorense* maintained a constant transpiration and photosynthesis longer, which is indicative of a more anisohydric behavior. This behavior maximizes resource acquisition and growth during slight drought, but leads to drop in water potential and catastrophic xylem embolism during more intense drought (Sperry 2003, McDowell *et al.* 2008, Skelton *et al.* 2015). In the genetic study conducted in parallel to this work, wilting symptoms have been associated with leaf transcriptional responses (Neji *et al.* 2019). The wilting of *E. suaveolens* has been related with the expression of many genes coding for signalling and metabolism-related pathways. The expression of these genes from the first signs of drought probably regulated the turgor loss of leaf cells and the early stomatal closure. A considerable regulation of these pathways was also found for *E. ivorense* in the latter stage of drought, confirming the delayed response of this species.

Wood-related hydraulic traits and stomatal regulation of gas exchanges are strongly involved in plant hydraulic failure under drought conditions, leading to tree mortality (Klein 2015, but see also Körner 2019). It is commonly hypothesized that, throughout evolutionary times, plants have increased their intrinsic embolism resistance to allow stomata to close later during drought, therefore maximising productivity (Klein 2014, Skelton *et al.* 2015, Anderegg *et al.* 2016). Our results are opposite to this assumption. In the previous chapter, we demonstrated the higher drought tolerance of the adult trees of *E. suaveolens* compared to *E. ivorense*, due to the combined action of a high resistance to embolism ($\Psi_{50,}$ the water potential at which the xylem experiences 50 % loss of xylem conductivity, of −3.88 ± 0.70 MPa for *E. suaveolens vs.* 1.93 ± 0.03 MPa for *E. ivorense*) and a desiccation delay-strategy at stem level (Gorel, Steppe, *et al.* 2019). In this chapter, we concluded that the seedlings of *E. suaveolens* exhibited a greater degree of stomatal control than that of *E. ivorense*, reducing transpiration from the first sign of drought. Under the assumption of the maintenance of stomatal behavior over developmental stage, these results supported the coordinated evolution of xylem resistance to embolism and desiccation delay strategies at stem and leaf levels. Up to now, not much work on the sensitivity of stomatal control in different-aged trees has been conducted. However, for *Quercus rotundifolia* and *Quercus faginea* (Fagaceae), it has been showed that mature trees had higher stomatal sensitivity to soil and atmospheric drought than seedlings (Mediavilla & Escudero 2004), supporting the maintenance and the strengthening of stomatal behavior over developmental stage.

The coordinated evolution of xylem resistance to embolism and stringent stomatal control have been recently demonstrated by Martin-StPaul *et al.* (2017) in a meta-analysis on 150 gymnosperm and angiosperm tree species covering a wide range of embolism resistance (Ψ_{50} ranged from -1.3 to -19 MPa). The authors suggested that this evolution resulted from selection pressures that have favored survival in drier environments over growth in wetter environments. Our results match with this interpretation, since we identified a trade-off between drought tolerance and growth between the two *Erythrophleum* species, interpreted as the key mechanism of niche evolution (**Chapter 4**, Gorel, Steppe, et al. 2019). The specialization to drier environments of the moist and dry forests species, *E. suaveolens*, has been promoted by the evolution of an overall highly conservative water use strategy, at stem and leaf levels. In contrast, *E. ivorense* displays an acquisitive strategy, maintaining high growth rate and, therefore, competitiveness for light in well-watered environments (Markesteijn & Poorter 2009, Gaviria & Engelbrecht 2015, Gaviria *et al.* 2017). We found that, compared to *E. suaveolens*, *E. ivorense* seedlings in well-watered condition had lower photosynthetic rate. It is possible that the poor lighting conditions during the experiment reduced the photosynthetic capacity of *E. ivorense*, however, it could also reflect the lower carbon demand of *E. ivorense* to build lightweight, low-cost organs.

The assimilation of respired CO_2 by stem photosynthesis has been hypothesised to play a crucial role in the resilience to drought, meeting the metabolic carbon demand of drought-stressed plants which have closed their stomata (Wittmann & Pfanz 2008) or have lost their leaves (Pfanz 2008, Eyles *et al.* 2009, Pivovaroff *et al.* 2016) and maintaining the hydraulic function of the xylem (Bloemen *et al.* 2016). In this study, we did not observe any difference between the “drought” and the “drought and packed” seedlings, either in terms of wilting or in terms of mortality. This suggests that stem photosynthesis does not play a crucial role in the drought-resistance of the two *Erythrophleum* species. The low number of seedling examined, however, has to be reminded. Nowadays, studies on woody tissue photosynthesis remain rare, especially for tropical trees (Santiago *et al.* 2016). In the future, further attention to understand the complete implication of woody tissue photosynthesis during drought stress will be necessary.

6

General discussion

1 The niche evolution of *Erythrophleum* and the mechanistic underpinnings

1.1 Our major findings

In this thesis, we aimed to understand the evolutionary processes that allowed particular tropical tree lineages to occur in vast areas, transcending habitats and biomes boundaries. While a diversity of methods at different phylogenetic and spatial scales can provide complementary insights, detailed analyses of well-resolved clades are needed to build robust generalizations about niche evolution and biome shifts (Donoghue & Edwards 2014). Therefore, from species distribution modeling to hard physiological measurements, we attempted to disentangle the processes behind the large-scale distribution of the *Erythrophleum* genus, which transcended significant ecological boundaries, resulting in biome shift from forest to savanna (**Chapter 2**, Gorel *et al.* 2015). Our results supported the substantial role of climate in niche evolution, and speciation, within the genus in Africa (**Chapter 3**). *Erythrophleum* has managed to adapt to extremely contrasted climates, resulting in a distribution encompassing biomes, from wet forest to dry forest and savanna. For *E. suaveolens*, the adaptation to drier environment was associated with the coordinated evolution of xylem resistance to embolism (**Chapter 4**, Gorel, Steppe, *et al.* 2019) and desiccation delay strategies at stem (**Chapter 4**) and leaf levels (**Chapter 5**). By confronting our results with previous studies on congeners, and specifically with the studies of Pittermann *et al.* (2012) on conifers (Cupressaceae), Pfautsch *et al.* (2016) and Bourne *et al.* (2017) on Eucalypt species (Myrtaceae), we believe that for certain tree lineages the lability of drought tolerance traits, specifically those related to xylem safety, is an important functional path allowing habitats and biome boundaries to be transcended.

1.2 The evidence of niche evolution

Using species distribution models, we showed that the climate, and specifically annual precipitation and annual temperature range, strongly constrained the distribution of the African *Erythrophleum* species, shaping the restricted range of *E. ivorense* in wet forest, the huge ecological amplitude of *E. suaveolens* across the moist and dry forests, and the association of *E. africanum* with the savanna (**Chapter 3**, Gorel, Duminil, *et al.* 2019). Our results supported the evolution of the genus along a rainfall-aridity gradient, boosted by past climate fluctuations (as theoretically developed by Rundle & Nosil (2005) and Donoghue & Edwards (2014), **Chapter 1**). The divergence date of *E. africanum,* the savanna species, can coincide with the aridification episodes of the mid-Pliocene (Liddy *et al.* 2016). While it remains difficult to conclude on the direction of past biome shifts, the exposure to drier climate could had promoted the diversification of the lineage and its transition into the savanna biome. One transition during the Pliocene from rain to dry forest has been already inferred for the African tropical tree genus *Guibourtia* (Fabaceae, Tosso 2018). Between *E. suaveolens* and *E. ivorense*, the mean divergence date (c. 650 ka, Duminil *et al.* 2015) is concomitant with the Pleistocene climatic cycles (Johnson *et al.* 2016) and the 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).

More surprisingly, we also found evidence of contrasted climatic niche between genetic populations within species. The climate-driven contractions of forests inside refuges during the Pleistocene (Collins *et al.* 2014, Lézine *et al.* 2019) have shaped genetic diversity within *Erythrophleum* species (Duminil *et al.* 2015). This result was confirmed for other species and genera by Hardy *et al.* (2013). In addition, we found that within *E. suaveolens* adaptive divergence also occurred (**Chapter 3**, Gorel, Duminil, *et al.* 2019). *Erythrophleum suaveolens* gene pools are distributed along rainfall gradients: on 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. We hypothesize that 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 (2017). Then, divergent selection induced local adaptation and the genetic diversification between populations, boosted by the absence of gene flow due to spatial isolation (Rundle & Nosil 2005). The ecological divergence between the *E. suaveolens* gene pools has been recently confirmed by inherent differences in wood and leaf traits, as first explored in a master’s thesis (Daher 2018).

In Africa, only a few studies examined the relationship between the distribution of congeneric plant species and climate (but see Dransfield & Uhl 2008, Blach-Overgaard *et al.* 2010, Couvreur *et al.* 2011, Holstein & Renner 2011). By modelling the environmental niches, we obtained evidences of the role of ecological adaptation through climate on the diversification of the *Erythrophleum* species and gene pools. However, we were also confronted with two main limits of the approach. First, species distribution models and the associated statistical tests for niche divergence are strongly dependent on the environmental factors retained in the analysis, and depend on a priori assumption on the relevant environmental axes of the niche (Graham *et al.* 2004, Guisan & Thuiller 2005). Secondly, these models do not allow the identification of the ecological processes and traits that underpin niche evolution. Within lineages, dissecting the functional traits and strategies provides the strongest evidence for niche evolution and allow the understanding of the mechanistic underpinnings of ecological transitions (Westoby 1998, Wiens & Donoghue 2004). Therefore, to precisely explore how related tropical tree species could evolve on a rainfall-aridity gradient, we compared the traits and performance of the two sister species *E. ivorense* and *E. suaveolens* using *in situ* measurements and a controlled experiment.

1.3 The functional understanding

In this thesis, we provided evidence for the coordinated evolution of xylem resistance to embolism and desiccation delay strategies, at both stem and leaf levels, as the key process behind the niche evolution of the two forest species of *Erythrophleum* (**Figure 6.1**).

The specialization to drier environment of the moist and dry forest species, *E. suaveolens*, has been promoted by vessel-associated traits, such as narrow vessels and intervessel pits, and high vessel cell-wall reinforcement, resulting in low vulnerability to drought-induced xylem embolism (**Chapter 4**, Gorel, Steppe, *et al.* 2019). In addition, two desiccation delay-strategies contributed to delay a fall in xylem pressure during drought: 1) an early stomatal closure, limiting water loss trough transpiration (**Chapter 5**), 2) an internal water supply of the xylem throughout dehydration, mainly because a large proportion of small vessels can serve as a water reservoir to mitigate drought-induced xylem tension (**Chapter 4**). This overall strong conservative water use strategy, however, comes at the cost of reducing growth rate, resulting in the competitive exclusion from wetter environments (Markesteijn & Poorter 2009, Gaviria & Engelbrecht 2015, Gaviria *et al.* 2017). By contrast, *E. ivorense* displays traits allowing high growth rate and, therefore, competitiveness for light in well-watered environments (**Chapters 4 and 5**). *Erythrophleum ivorense* wood traits allowed high hydraulic efficiency (Tyree *et al.* 1994, Sperry *et al.* 2008, Anderegg & Meinzer 2015). In addition, during short dry periods or daily fluctuations in vapor-pressure deficit, the high hydraulic capacitance of *E. ivorense* could maintained the stem water potential (**Chapter 4**), allowing a constant transport of water for photosynthesis, while avoiding catastrophic embolism formation.

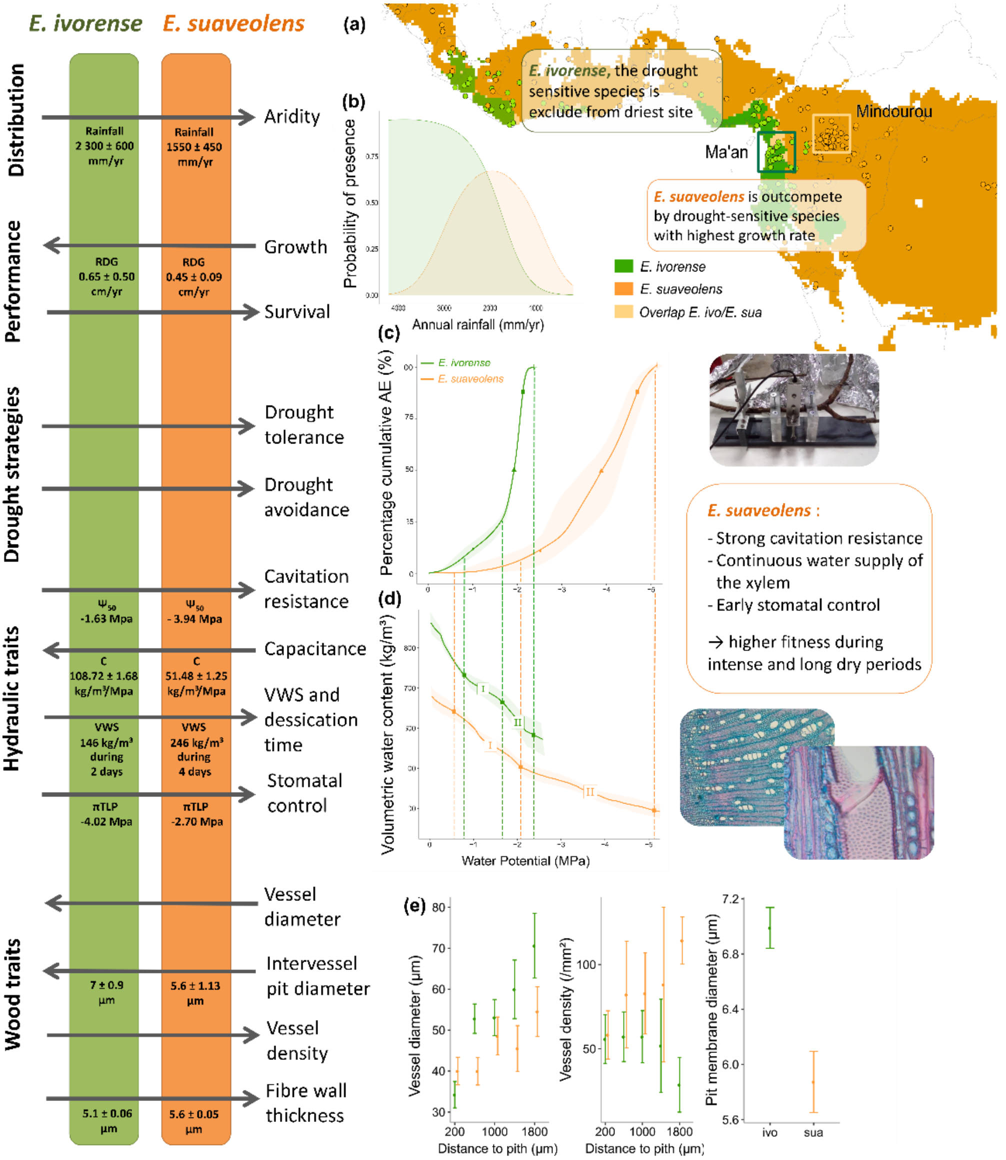


Figure 6.1 A mechanistic understanding of the niche evolution between *E. ivorense* (green, wet forest) and *E. suaveolens* (orange, moist and dry forests), from wood traits to distribution. Distribution in Upper and Lower Guinea (a) and response curve (probability of presence) along the rainfall gradient (b); occurrence data overlaid on the map. Acoustic vulnerability curves (c) and desorption curves (d). The vulnerability thresholds AE_{12} (circle), AE_{50} (triangle), AE_{88} (square) and AE_{100} (cross) are indicated as well. Phases I and II are delimited by vertical lines and the slopes within these phases represent elastic (C_{el}) and inelastic (C_{inel}) hydraulic capacitance, respectively. Average (and 95% confidence intervals) of vessel diameter and vessel density from pith to bark and of pit membrane diameter measured on branches (e).

And the savanna species?

Unfortunately, we did not include the African (*E. africanum*, *E. lasianthum*) and Australian (*E. chlorostachys*) savanna species in the *in situ* measurements and in the controlled experiment. However, available data on growth, wood density and stature of *E. africanum* (**Chapter 2**) were in accordance with the trade-off between growth and drought tolerance mentioned above and that can explain its exclusion from wetter forest sites and its persistence under the drier conditions of the savanna biome. The high wood density (0.85 ± 0.04 g/cm^3 following Zanne *et al.* 2009) and the shorter stature (4-12 m height according to Brenan 1967) of *E. africanum* suggested a lower susceptibility to drought compared to the forest species. Indeed, high wood density has been associated to smaller vessels resulting in lower vulnerability to xylem drought-induced embolism (Hacke *et al.* 2001, Markesteijn, Poorter, Bongers, *et al.* 2011) and a shorter stature is expected to reduce the inherent vulnerability to hydraulic stress (Ryan *et al.* 2006, Meinzer *et al.* 2011). In return, the shorter stature and the lower growth rate of *E. africanum* (0.15 cm/yr according to Holdo 2006) easily explain its exclusion from wetter forest sites, outcompeted by trees with higher competitiveness for light in environments characterized by high and closed canopy. However, the importance of these traits in the evolution of *E. lasianthum* in Africa and even more in the evolution of other *Erythrophleum* species worldwide, such as *E. chlorostachys* in Australia, remains to be validated.

1.4 The lability of drought-resistance traits

We still lack critical tests to conclude on the importance of shifts in drought-resistance traits and strategy in the diversification of tropical woody lineages. For tropical trees, drought response strategies have been explored, but on taxa that vary widely in evolutionary history (*e.g.* Poorter & Markesteijn 2008, Sterck *et al.* 2014, Wolfe & Kursar 2015), confusing the effects of environments with the effects of phylogenetic conservatism (Pfautsch *et al.* 2016). To our knowledge, the association between the lability of drought-resistance traits and the diversification of tree lineages has only been explored on conifers (Pittermann *et al.* 2012 for the Cupressaceae, Larter *et al.* 2017 for the *Callitris* genus) and Eucalypt in Australia (Pfautsch *et al.* 2016, Bourne *et al.* 2017, Li *et al.* 2019). For these clades, shifts toward wood traits that allow greater xylem resistance to embolism have been associated with radiation into dry environments (Pittermann *et al.* 2012, Pfautsch *et al.* 2016, Larter *et al.* 2017), strengthening our belief that, even if only tested for two tropical species, the lability of wood structural traits involved in xylem safety is a key factor allowing niche evolution along rainfall-aridity gradient. Within the *Eucalypts* genus, xylem resistance to embolism in drier conditions has been associated with the reduction of stomatal control during water shortage (*i.e.* a more anisohydric strategy, Bourne *et al.* 2017, Li *et al.* 2019). This is in contrast with our results for *Erythrophleum*, suggesting that different associations of stem and leaf hydraulic traits may be involved in diversification along rainfall-aridity gradients.

2 The generalization to other genera

2.1 The niche evolution of the tropical African woody flora

We have accumulated evidence of niche evolution along climatic gradients for the *Erythrophleum* genus, however, the extent to which this pattern could be generalized to other woody genera in Africa still has to be investigated. In the introduction of this thesis, we provided some baseline evidence suggesting that genera with large distribution, encompassing forest and savanna biomes, are not rare, as early recognized by White (1978) for *Diospyros spp.* To take the analysis a little further, we developed a five-step approach (**Figure 6.2**) to identify niche evolution and biome shift within a large set of woody genera in subtropical Africa.

Step [1] Distribution and climate data. First, we extracted from the RAINBIO dataset (Sosef 1994, Droissart *et al.* 2018, a recent compilation of herbarium records across tropical Africa) the occurrence of the woody species present in the forest and savanna sites studied by Fayolle *et al.* (2014, 2018). Then, we assembled climatic data for subtropical Africa using the 19 climatic variables of the BIOCLIM dataset (from the ‘WorldClim’ Global Climate database, Hijmans *et al.* 2005).

Step [2] Niche modeling. For the 1439 species with at least 10 occurrences (belonging to 532 genera), we modeled the climatic niche using the approach developed by Broennimann *et al.* (2012). This approach allowed delineating the climate envelope of each species along two environmental gradients, rainfall and temperature, defined by the first two axes of a Principal Component Analysis (**Figure 6.3**).

Step [3] Pairwise niche overlap and dissimilarity. The Schoener’s D statistic (Schoener 1968, Warren *et al.* 2008) was used to quantify niche overlap (O) among all pairs of species. The overlap varies between 0 (no overlap) and 1 (complete overlap, similar niches). The corresponding dissimilarity matrix (1-O) was built, *i.e.* a half symmetric matrix composed of 1439 species × 1439 species, and containing the value of niche dissimilarity (how different climatic niches are) between all pairs of species.

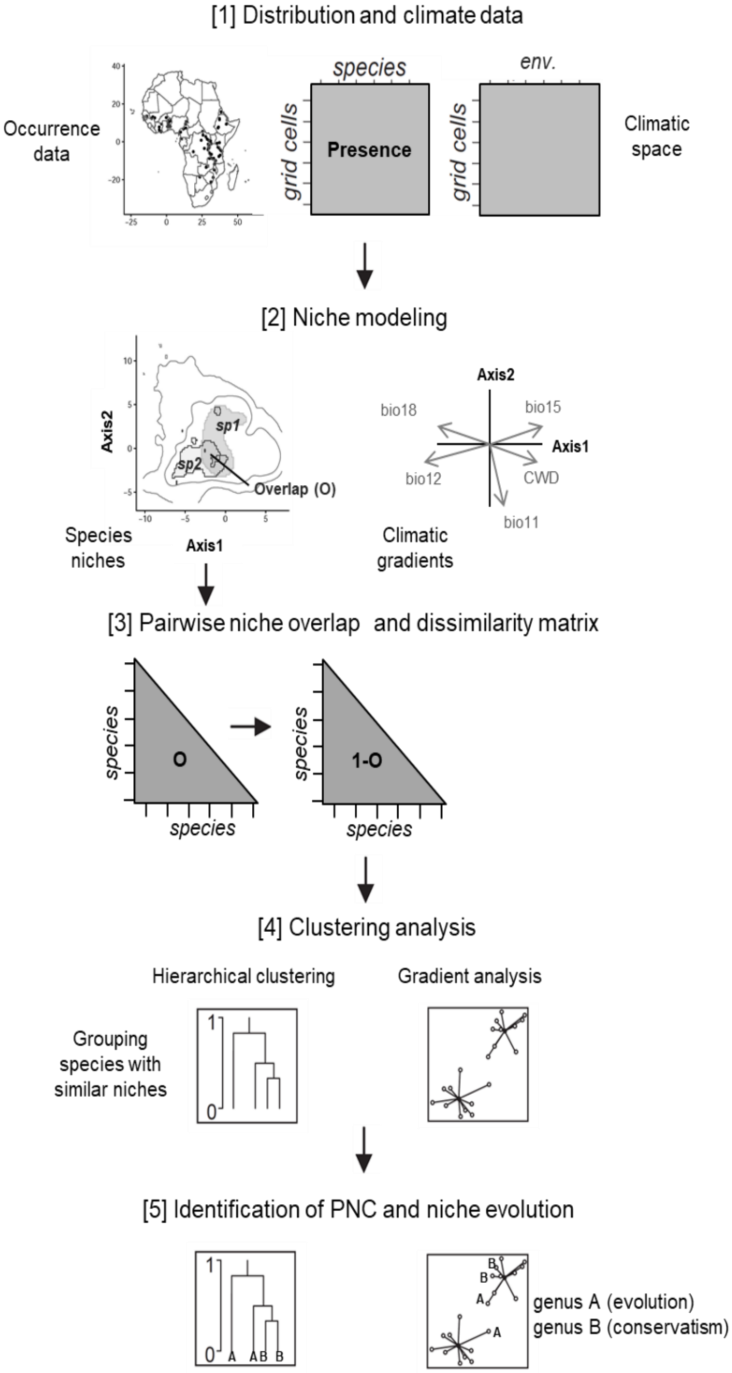


Figure 6.2 Conceptual diagram of analysis steps. Numbers in brackets correspond to the analysis steps described in the text.

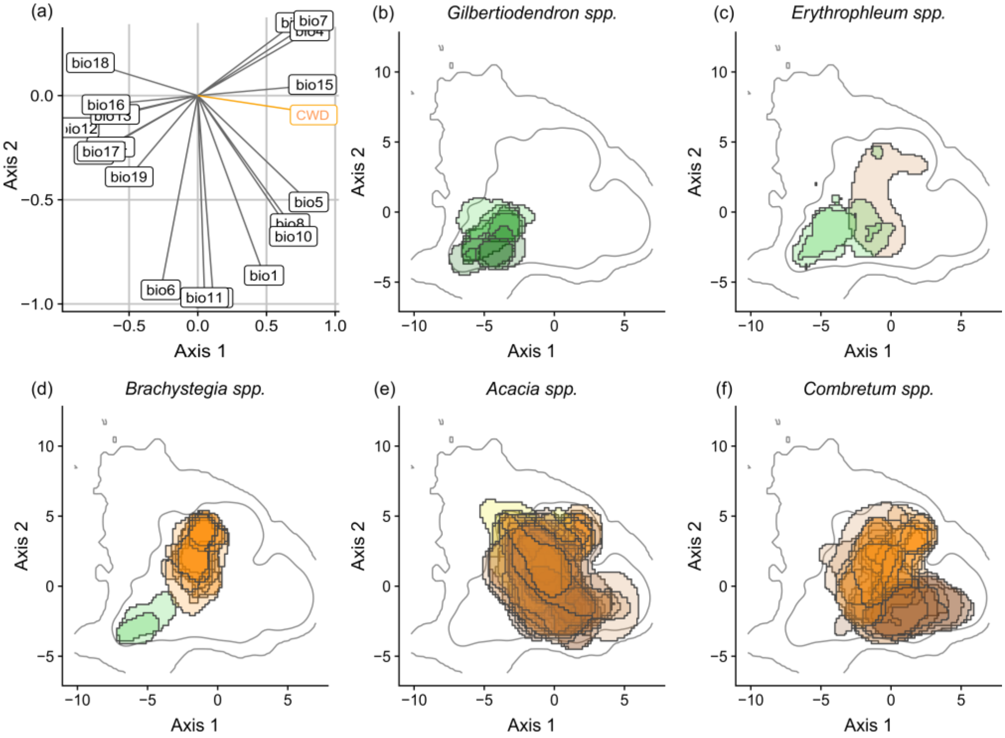


Figure 6.3 Environmental gradients and climatic niches of congeneric species belonging to 5 genera. The contribution of the climatic variables on the two axes of the PCA is represented (a). Each panel represents the niches of congeneric species along the two first axes of the PCA (b-f). The color coding matches the dendrogram in **Figure 6.4**, with green colors associated with the forest biome and orange-brown colors with the savanna biome.

Step [4] Clustering analysis. A hierarchical clustering analysis was used for grouping species with the same climatic niche, occupying similar climates but not necessarily found in the same areas. We used Ward's algorithm for creating the dendrogram representing niche dissimilarity among species. We decided to keep seven groups of species, examining spatial and climatic distribution of the groups formed at each step, from two groups (opposing forest and savanna species) and up to 12 groups. Among the seven groups retained, three groups of species are associated with the forest biome and four groups of species with the savanna biome (**Figure 6.4a**). An ordination technique, the Nonmetric Multidimensional Scaling (NMDS) using dissimilarity as input (1-O), was used to plot niche dissimilarity among species in two dimensions. The ordination allowed identifying the gradients across the seven groups of species identified with the clustering (**Figure 6.4b**).

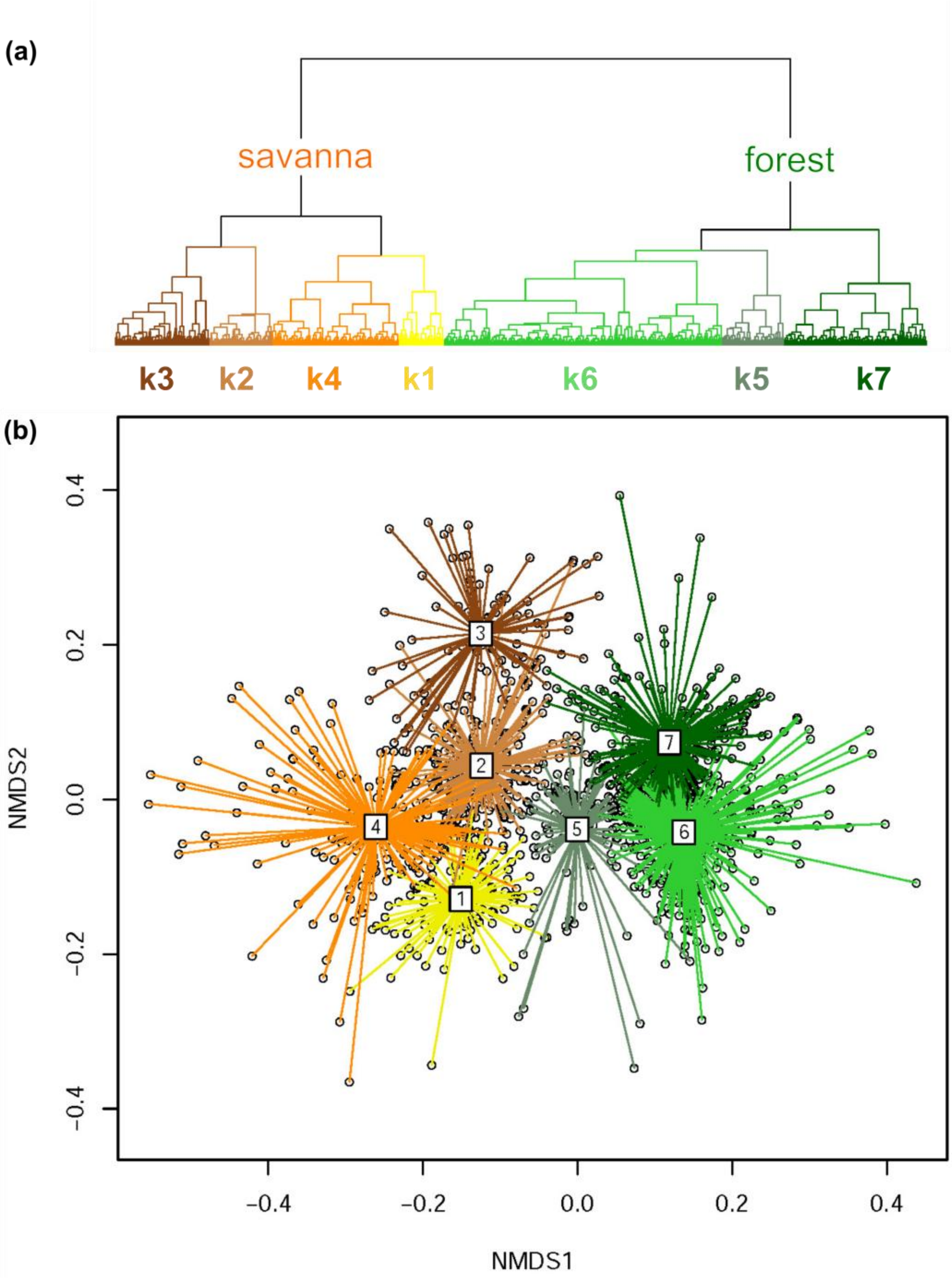


Figure 6.4 Hierarchical clustering of 1439 species on the basis of shared climatic niches (a), the first division corresponds to the forest and the savanna biome. Nonmetric Multidimensional Scaling (NMDS) representing niche dissimilarity among the 1439 species in two dimensions (b), with same color coding as in the dendrogram (a) for seven species clusters (k1-7).

Step [5] PNC and niche evolution. We finally examined the distribution of congeneric species into the dendrogram and on the ordination. Specifically, we identified genera with conserved niche, indicative of Phylogenetic Niche Conservatism (PNC), and diversified genera occupying contrasted climatic niche, indicative of niche evolution. We finally quantified niche shifts for each genus, between the forest and the savanna biomes (for two groups of species, k=2, **Figure 6.5b**), and within the forest and savanna biomes (for seven groups of species, k=7, **Figure 6.6**).

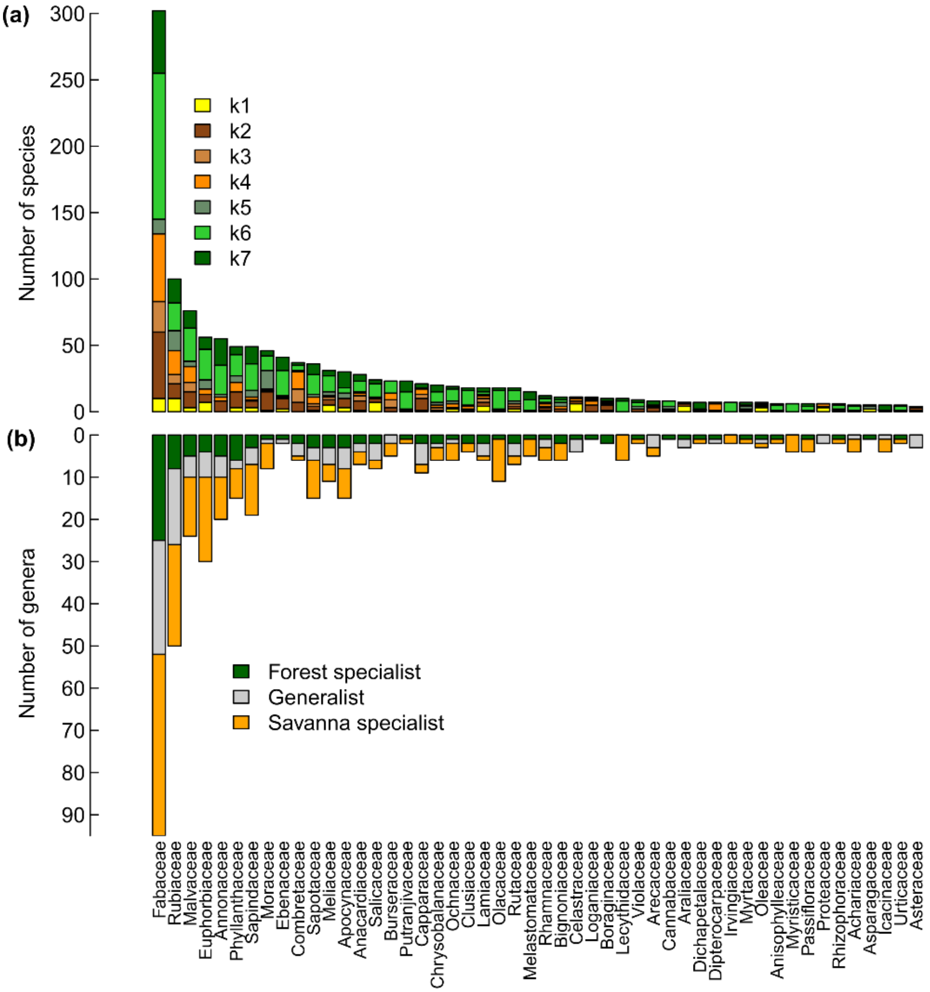


Figure 6.5 (a) Number of species per family assigned to each cluster. (b) Number of genera per family that are savanna specialist (“savanna” niche conservatism), forest specialist (“forest” niche conservatism) or generalist, making the transition between the two biomes. Only the 50 most diversified families are shown. The color coding matches the dendrogram and ordination in **Figure 6.4**.

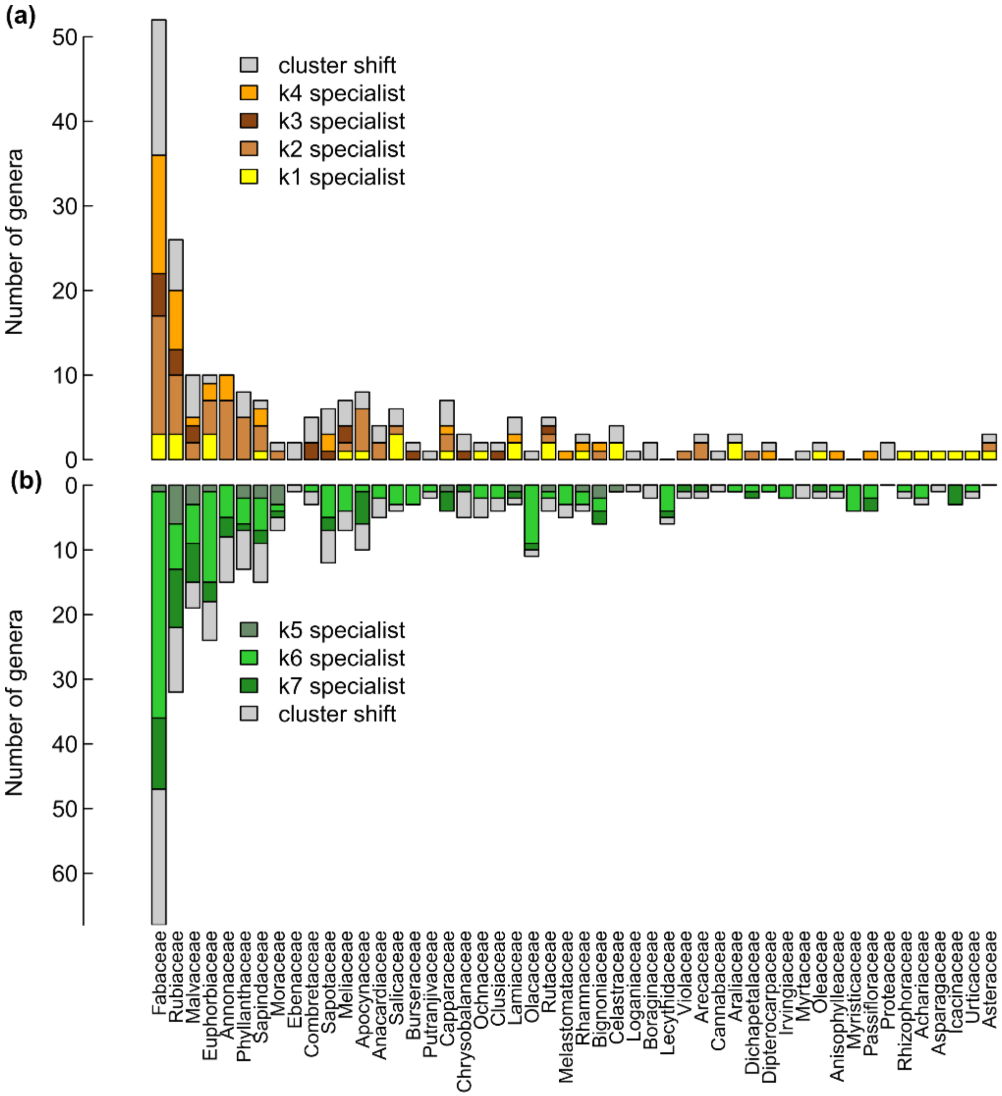


Figure 6.6 Within the savanna biome (a) and within the forest biome (b), number of genera per family that are specialist of only one cluster and number of genera per family making at least one transition between two clusters. Only the 50 most diversified families are shown. The color coding matches the ordination in **figure 6.4**).

We identified more than 110 African woody genera (20% of the genera studied) with both forest and savanna species (**Figure 6.5b**). The biome shift between forest and savanna is thus not rare as already reported (Linder 2014). Forest and savanna have almost no species in common as reported by plot-based studies in Ghana (Swaine *et al.* 1976) and South Africa (Charles-Dominique *et al.* 2015), but they share many genera. In our species set, the most represented family is the hyperdiverse Fabaceae family, with 25 genera (26% of the Fabaceae genera) that have managed to evolve and overcome the steep ecological transition between the forest and savanna biomes. Among them, there is *Erythrophleum* (**Figure 6.3c**), our study model, and *Brachystegia* (**Figure 6.3d**), generally associated with African savannas but also containing two dense forest species (Linder 2014). In the same family, we also identified biome-specialist genera, such as *Gilbertiodendron*, a forest-specialist genus (**Figure 6.3a**) and *Acacia,* a savanna-specialist (**Figure 6.3e**). We are aware that the *Acacia* genus has been revised and split into *Vachellia* and *Senegalia* in Africa (Kyalangalilwa *et al.* 2013), this update is, however, not implemented in the African Plant Database (http://www.ville-ge.ch/musinfo/bd/cjb-/africa/recherche.php) and in the RAINBIO dataset. This example reflects the limits of large datasets, which may not be up to date with taxonomic revisions and could also include some taxonomic misidentifications. Within biomes, niche evolution is also common, with congeneric species belonging to different clusters of species involving 82 genera over the 266 found in the savanna biome (**Figure 6.6a**) and 122 genera over the 379 found in the forest biome (**Figure 6.6b**).

Although these results are preliminary, they strongly support the niche evolution within many woody lineages in tropical Africa. Although Phylogenetic Niche Conservatism has been commonly reported (Crisp *et al.* 2009, Peterson 2011, Linder 2014), climatic niches might be more labile than expected. As done in this thesis for our study model, *Erythrophleum,* the mechanistic underpinnings that allowed these lineages to diversify into novel environments remain to be explored. Combining hard ecophysiological measurements, and soft traits, more easily measurable in the field, is the way forward.

2.2 The exploration of functional shifts within lineages

While the co-evolution of wood and leaf traits involving in xylem safety and desiccation delay strategies has been associated with the niche evolution of *Erythrophleum* and *Eucalyptus* (Pfautsch *et al.* 2016, Bourne *et al.* 2017, Li *et al.* 2019), the implication of other traits in the diversification of tropical tree lineages deserves attention. Specifically, desiccation-delay traits such as leaf deciduousness and biomass allocation to roots have been previously mentioned (Santiago *et al.* 2016). Deciduousness is a key feature of tropical forests, specifically in Central Africa (Ouédraogo *et al.* 2016). It has been known for a long time that forests on the dry side of precipitation gradients commonly have a higher proportion of deciduous canopy species (Schimper 1903). Compositional change toward deciduous species has been recently observed in Ghana after decades of drying trends (Fauset *et al.* 2012, Aguirre-Gutiérrez *et al.* 2019). Deciduousness reduces whole-plant transpiration and respiration during dry season, reducing the risk of embolism. For root traits, it has been proved that large investment in coarse roots improves soil water capture during drought and permits resprouting following drought (Hoffmann *et al.* 2003, Hoffmann & Franco 2008). However, there are still few studies on species phenology and biomass allocation to roots across phylogenies.

Bark thickness, reproductive height and spinessence have also been related to transition into the savanna biome (Bond 2008, Hoffmann & Franco 2008). The savanna biome, characterized by frequent fires and herbivory (Bond 2008, Staver *et al.* 2011), promoted the evolution of thicker barks, reducing the risk of stem death during fires (Hoffmann *et al.* 2003). The reduction of reproductive height allows reaching maturity quicker, and thus between consecutive fires (Hoffmann *et al.* 2003). Finally, spinessence constitutes the best safeguard against herbivory (Charles-Dominique *et al.* 2015). Nowadays, the increasing availability of trait data in literature and database (such as TRY, Kattge *et al.* 2011) have opened the way for a general exploration of the major evolutionary shifts allowing lineages to transcend habitat and biome boundaries, though trait measurement campaigns are still needed for largely unexplored areas such Central Africa.

3 To conclude, some practical implications

In addition to knowledge on niche evolution, this work allows to provide some management advices. Planting timber species in logging gaps and/or restoring degraded forest areas are effective techniques to maintain and favor the populations of species with high commercial values. For choosing the right species/provenance to plant in the right place, our results suggest to examine not only the immediate performance but the entire species ecology, especially since climate is changing rapidly (Pachauri *et al.* 2015). The choice of species/provenance must result from a trade-off between productivity and risk.

The two forests species, *E. ivorense* and *E. suaveolens* are widely used for timber in Central Africa, traded under the same commercial name, Tali, and also used by local populations for traditional medicine (Gorel et al. 2015). Like other light-demanding timber species, such as *Pericopsis elata* (Fabaceae) and *Milicia excelsa* (Moraceae), enhancing regeneration is needed for sustainable management (Fayolle *et al.* 2015, Doucet *et al.* 2016). Despite the higher inherent growth of the wet forest species *E. ivorense* compared to *E. suaveolens* (**Chapter 3**), we do not recommend its plantation in non-native and drier habitats. We demonstrated in this work that, for this species, higher growth rate comes at the cost of severe reduction of drought resistance (**Chapters 3** and **4**). *Erythrophleum ivorense* will certainly not survive intense drought, more likely to occur in these regions and that will be more frequent in the future, as already observed in West Africa, and already inducing changes in forest composition (Fauset *et al.* 2012, Aguirre-Gutiérrez *et al.* 2019). In contrast, the plantation in native, and also in wetter habitats, of the highly drought tolerant species, *E. suaveolens* (**Chapters 3** and **4**), could be advantageous to anticipate the effects of global warming. In its native habitat (South-Eastern Cameroon), *E. suaveolens* has already shown good performance in plantation, in comparison to other 22 species (Doucet *et al.* 2016). In wetter and non-native habitats, sylvicultural practices should probably be applied to reduce the overstory density and limit competition with fast-growing species (**Chapters 3**).

Collecting ecological data from multi-site provenance trials and arboreta for as many timber tree species as possible would help choosing species and also provenance for plantation. Defining sylvicultural guidelines is also important, but tremendously missing in Central Africa. However, while only growth is traditionally monitored in plantations, we recommend going further, and extending the approach we conducted in this thesis. It would be worth measuring drought-related physiological traits, such as the vulnerability to embolism and the water potential at leaf turgor loss (π_{TLP}, an easily quantifiable proxy of stomatal control), to quantify species drought sensitivity. These physiological measurements are costly and require specific equipment, but the results are almost immediate and could help anticipate drought-induced mortality only observed over the long-term. Indeed, drought sensitivity increases with tree height and could lead to mortality only at mature stage (Ryan & Yoder 1997). For instance, though benefitting from an 8-year plantation trial in South-East Cameroon, it is still difficult to conclude on the best provenance. A provenance of *E. suaveolens* (Ouesso, Congo Republic) grows faster than the others (**Appendix 1**), but possibly at the expense of drought tolerance (**Chapters 3** and **4**). While choosing this provenance for plantation would maximize productivity, the increase of the risk cannot be evaluated without the quantification of the drought-related traits.

References

ACKERLY, D. D. 2003. Community Assembly, Niche Conservatism, and Adaptive Evolution in Changing Environments. Int. J. Plant Sci. 164: S165–S184.

AGUIRRE-GUTIÉRREZ, J., I. OLIVERAS, S. RIFAI, S. FAUSET, S. ADU-BREDU, K. AFFUM-BAFFOE, T. R. BAKER, T. R. FELDPAUSCH, A. GVOZDEVAITE, W. HUBAU, N. J. B. KRAFT, S. L. LEWIS, S. MOORE, Ü. NIINEMETS, T. PEPRAH, O. L. PHILLIPS, K. ZIEMIŃSKA, B. ENQUIST, and Y. MALHI. 2019. Drier tropical forests are susceptible to functional changes in response to a long-term drought. Ecol. Lett. 22: 855–865.

AKINDELE, S. O., and V. M. LEMAY. 2006. Development of tree volume equations for common timber species in the tropical rain forest area of Nigeria. For. Ecol. Manag. 226: 41–48.

AKINPELU, B. A., C. A. DARE, F. I. ADEBESIN, E. O. IWALEWA, and O. O. OYEDAPO. 2013. Effect of stem-bark of Erythrophleum suaveolens (Guill. & Perri.) saponin on fresh water snail (Lanistes lybicus) tissues. Afr. J. Environ. Sci. Technol. 6: 446–451.

AKOÈGNINOU, A., W. J. VAN DER BURG, L. J. G. VAN DER MAESEN, V. ADJAKIDJÈ, J. P. ESSOU, B. SINSIN, and H. YÉDOMONHAN. 2006. Flore analytique du Bénin. Backhuys Publishers, Wageningen.

ALLOUCHE, O., A. TSOAR, and R. KADMON. 2006. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). J. Appl. Ecol. 43: 1223–1232.

ANDEREGG, W. R. L. 2015. Spatial and temporal variation in plant hydraulic traits and their relevance for climate change impacts on vegetation. New Phytol. 205: 1008–1014.

ANDEREGG, W. R. L., T. KLEIN, M. BARTLETT, L. SACK, A. F. A. PELLEGRINI, B. CHOAT, and S. JANSEN. 2016. Meta-analysis reveals that hydraulic traits explain cross-species patterns of drought-induced tree mortality across the globe. Proc. Natl. Acad. Sci. 113: 5024–5029.

ANDEREGG, W. R. L., and F. C. MEINZER. 2015. Wood Anatomy and Plant Hydraulics in a Changing Climate. In U. Hacke (Ed.) Functional and Ecological Xylem Anatomy. pp. 235–253, Springer International Publishing.

ANDERSON, R. P. 2003. Real vs. artefactual absences in species distributions: tests for Oryzomys albigularis (Rodentia: Muridae) in Venezuela. J. Biogeogr. 30: 591–605.

ANHUF, D., M.-P. LEDRU, H. BEHLING, F. W. DA CRUZ, R. C. CORDEIRO, T. VAN DER HAMMEN, I. KARMANN, J. A. MARENGO, P. E. DE OLIVEIRA, L. PESSENDA, A. SIFFEDINE, A. L. ALBUQUERQUE, and P. L. DA SILVA DIAS. 2006. Paleo-environmental change in Amazonian and African rainforest during the LGM. Palaeogeogr. Palaeoclimatol. Palaeoecol. 239: 510–527.

ARBONNIER, M. 2009. Arbres, arbustes et lianes des zones sèches d’Afrique de l’Ouest. Éditions Quæ, Versailles, France.

AUBRÉVILLE, A. 1932. La forêt de la Côte d’Ivoire: Essai de gèobotanique forestière. Comité d’études historiques et scientifiques de l’Afrique occidentale française.

AUBRÉVILLE, A. 1950. Flore forestière soudano-guinéenne. Société d’éditions géographiques, maritimes et coloniales, Paris, France.

AUBRÉVILLE, A. 1959. La Flore forestière de la Côte d’Ivoire 2nd ed. Centre Technique Forestier Tropical, Nogent-sur-Marne, France.

AUBRÉVILLE, A. 1962. Position chorologique du Gabon. Flore Gabon 3: 3–11.

AUBRÉVILLE, A. 1968. Flore du Gabon: Légumineuses. Caesalpinioidées. Muséum Nat. d’Histoire Naturelle, Laboratoire de Phanérogamie, Paris, France.

AUBRÉVILLE, A. 1970. Légumineuses-Caesalpinioidées, Flore du Cameroun. Muséum National d’Histoire Naturelle, Paris, France.

ÁVILA-LOVERA, E., A. J. ZERPA, and L. S. SANTIAGO. 2017. Stem photosynthesis and hydraulics are coordinated in desert plant species. New Phytol. 216: 1119–1129.

BALDWIN, R. A. 2009. Use of Maximum Entropy Modeling in Wildlife Research. Entropy 11: 854–866.

BARDGETT, R. D., L. MOMMER, and F. T. DE VRIES. 2014. Going underground: root traits as drivers of ecosystem processes. Trends Ecol. Evol. 29: 692–699.

BEECKMAN, H. 2016. Wood anatomy and trait-based ecology. IAWA J. 37: 127–151.

BEHEREGARAY, L. B., G. M. COOKE, N. L. CHAO, and E. L. LANDGUTH. 2015. Ecological speciation in the tropics: insights from comparative genetic studies in Amazonia. Front. Genet. 5.

BILÉ ALLOGHO, J. 1999. Étude sur les ressources forestières du Gabon. FAO, Rome, Italie.

BIVAND, R., and C. RUNDEL. 2014. rgeos: Interface to Geometry Engine–Open Source (GEOS). R Package Version 0.3–6. Vienna Compr. R Arch. Netw. Softw.

BLACH-OVERGAARD, A., W. D. KISSLING, J. DRANSFIELD, H. BALSLEV, and J.-C. SVENNING. 2013. Multimillion-year climatic effects on palm species diversity in Africa. Ecology 94: 2426–2435.

BLACH-OVERGAARD, A., J.-C. SVENNING, J. DRANSFIELD, M. GREVE, and H. BALSLEV. 2010. Determinants of palm species distributions across Africa: the relative roles of climate, non-climatic environmental factors, and spatial constraints. Ecography 33: 380–391.

BLOEMEN, J., L. L. VERGEYNST, L. OVERLAET-MICHIELS, and K. STEPPE. 2016. How important is woody tissue photosynthesis in poplar during drought stress? Trees 30: 63–72.

BOND, W. J. 2008. What Limits Trees in C4 Grasslands and Savannas? Annu. Rev. Ecol. Evol. Syst. 39: 641–659.

BONGERS, F., L. POORTER, R. S. A. R. VAN ROMPAEY, and M. P. E. PARREN. 1999. Distribution of twelve moist forest canopy tree species in Liberia and Côte d'Ivoire: response curves to a climatic gradient. J. Veg. Sci. 10: 371–382.

BORCHERT, R. 1994. Soil and Stem Water Storage Determine Phenology and Distribution of Tropical Dry Forest Trees. Ecology 75: 1437–1449.

BORCHERT, R. 1998. Responses of Tropical Trees to Rainfall Seasonality and its Long-Term Changes. Clim. Change 39: 381–393.

BORCHERT, R., and W. T. POCKMAN. 2005. Water storage capacitance and xylem tension in isolated branches of temperate and tropical trees. Tree Physiol. 25: 457–466.

BOURNE, A. E., D. CREEK, J. M. R. PETERS, D. S. ELLSWORTH, and B. CHOAT. 2017. Species climate range influences hydraulic and stomatal traits in Eucalyptus species. Ann. Bot. 120: 123–133.

BOX, E. O. 2016. World Bioclimatic Zonation. In E. O. Box (Ed.) Vegetation Structure and Function at Multiple Spatial, Temporal and Conceptual Scales. Geobotany Studies. pp. 3–52, Springer International Publishing, Cham.

BRENAN, J. P. M. 1967. Flora of tropical east Africa, Leguminosae, subfamily Caesalpinioideae. Crown Agents, London, United Kingdom.

BRENES-ARGUEDAS, T., P. D. COLEY, and T. A. KURSAR. 2009. Pests vs. Drought as Determinants of Plant Distribution along a Tropical Rainfall Gradient. Ecology 90: 1751–1761.

BRICE, K. A., B. J. AKHANOVNA, and B. ANOUBILÉ. 2011. Erythrophleum africanum Afzel.(Caesalpiniaceae), an African toothpick: Phytochemical screening, total flavonoid content and antioxidant activity. J. Med. Plants Res. 5(27): 6273–6277.

BRODERSEN, C., and A. MCELRONE. 2013. Maintenance of xylem Network Transport Capacity: A Review of Embolism Repair in Vascular Plants. Front. Plant Sci. 4.

BRODRIBB, T. J., and H. COCHARD. 2009. Hydraulic Failure Defines the Recovery and Point of Death in Water-Stressed Conifers. Plant Physiol. 149: 575–584.

BROENNIMANN, O., M. C. FITZPATRICK, P. B. PEARMAN, B. PETITPIERRE, L. PELLISSIER, N. G. YOCCOZ, W. THUILLER, M.-J. FORTIN, C. RANDIN, N. E. ZIMMERMANN, C. H. GRAHAM, and A. GUISAN. 2012. Measuring ecological niche overlap from occurrence and spatial environmental data. Glob. Ecol. Biogeogr. 21: 481–497.

BURKILL, H. M. 1995. The useful plants of west tropical Africa, Vols. 1-3. Royal Botanic Gardens, Kew, Richmond, United Kingdom.

CHARLES-DOMINIQUE, T., A. C. STAVER, G. F. MIDGLEY, and W. J. BOND. 2015. Functional differentiation of biomes in an African savanna/forest mosaic. South Afr. J. Bot. 101: 82–90.

CHAVE, J., D. COOMES, S. JANSEN, S. L. LEWIS, N. G. SWENSON, and A. E. ZANNE. 2009. Towards a worldwide wood economics spectrum. Ecol. Lett. 12: 351–366.

CHEVALIER, A. 1916. La forêt et les bois du Gabon. A. Challamel, Paris, France.

CHIDUMAYO, E. N., and D. J. GUMBO. 2010. The dry forests and woodlands of Africa: managing for products and services. Earthscan, London, United Kingdom ; Washington, USA.

CHILDES, S. L. 1988. Phenology of nine common woody species in semi-arid, deciduous Kalahari Sand vegetation. Vegetatio 79: 151–163.

CHOAT, B. ET AL. 2012. Global convergence in the vulnerability of forests to drought. Nature 491: 752–5.

CHOAT, B., T. W. BRODIE, A. R. COBB, M. A. ZWIENIECKI, and N. M. HOLBROOK. 2006. Direct measurements of intervessel pit membrane hydraulic resistance in two angiosperm tree species. Am. J. Bot. 93: 993–1000.

CHOAT, B., A. R. COBB, and S. JANSEN. 2008. Structure and function of bordered pits: new discoveries and impacts on whole-plant hydraulic function. New Phytol. 177: 608–626.

CHOAT, B., L. SACK, and N. M. HOLBROOK. 2007. Diversity of hydraulic traits in nine Cordia species growing in tropical forests with contrasting precipitation. New Phytol. 175: 686–698.

CIRAD. 2008. Tropix 7. Available at: http://tropix.cirad.fr/.

COLLINS, J. A., E. SCHEFUß, A. GOVIN, S. MULITZA, and R. TIEDEMANN. 2014. Insolation and glacial–interglacial control on southwestern African hydroclimate over the past 140 000 years. Earth Planet. Sci. Lett. 398: 1–10.

CORNELISSEN, J. H. C., S. LAVOREL, E. GARNIER, S. DÍAZ, N. BUCHMANN, D. E. GURVICH, P. B. REICH, H. TER STEEGE, H. D. MORGAN, M. G. A. VAN DER HEIJDEN, J. G. PAUSAS, and H. POORTER. 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. Aust. J. Bot. 51: 335–380.

COUVREUR, T. L., F. FOREST, and W. J. BAKER. 2011. Origin and global diversification patterns of tropical rain forests: inferences from a complete genus-level phylogeny of palms. BMC Biol. 9: 44.

CRISP, M. D., M. T. K. ARROYO, L. G. COOK, M. A. GANDOLFO, G. J. JORDAN, M. S. MCGLONE, P. H. WESTON, M. WESTOBY, P. WILF, and H. P. LINDER. 2009. Phylogenetic biome conservatism on a global scale. Nature 458: 754–756.

DAHER, N. 2018. Explaining the distribution patterns of morphologically similar species and gene pools of a tropical tree genus (Erythrophleum) using functional and life-history trait approach. Master thesis. Gembloux Agro-Bio Tech, University of Liege, Gembloux, Belgium.

DAMASCENO, R., M. L. STRANGAS, A. C. CARNAVAL, M. T. RODRIGUES, and C. MORITZ. 2014. Revisiting the vanishing refuge model of diversification. Front. Genet. 5: 1–12.

DE BAERDEMAEKER, N. J. F., R. L. SALOMÓN, L. DE ROO, and K. STEPPE. 2017. Sugars from woody tissue photosynthesis reduce xylem vulnerability to cavitation. New Phytol. 216: 720–727.

DE WOLF, J. 1998. Species composition and structure of the woody vegetation of the Middle Casamance region (Senegal). For. Ecol. Manag. 111: 249–264.

DEBLAUWE, V., V. DROISSART, R. BOSE, B. SONKÉ, A. BLACH-OVERGAARD, J.-C. SVENNING, J. J. WIERINGA, B. R. RAMESH, T. STÉVART, and T. L. P. COUVREUR. 2016. Remotely sensed temperature and precipitation data improve species distribution modelling in the tropics: Remotely sensed climate data for tropical species distribution models. Glob. Ecol. Biogeogr. 25: 443–454.

DENYS, E. 1980. A tentative phytogeographical division of tropical Africa based on a mathematical analysis of distribution maps. Bull. Jard. Bot. Natl. Belg. Van Natl. Plantentuin Van Belg. 465–504.

DETIENNE, P., F. OYONO, L. DURRIEU DE MADRON, B. DEMARQUEZ, and R. NASI. 1998. L’analyse de cernes : application aux études de croissance de quelques essences en peuplements naturels de forêt dense africaine. CIRAD-Forêt, Montpellier, France.

DEXTER, K. G., R. T. PENNINGTON, A. T. OLIVEIRA-FILHO, M. L. BUENO, P. L. SILVA DE MIRANDA, and D. M. NEVES. 2018. Inserting Tropical Dry Forests Into the Discussion on Biome Transitions in the Tropics. Front. Ecol. Evol. 6.

DIABATE, M., A. MUNIVE, S. M. DE FARIA, A. BA, B. DREYFUS, and A. GALIANA. 2005. Occurrence of nodulation in unexplored leguminous trees native to the West African tropical rainforest and inoculation response of native species useful in reforestation. New Phytol. 166: 231–239.

DIAZ, S. ET AL. 2004. The plant traits that drive ecosystems: Evidence from three continents. J. Veg. Sci. 15: 295–304.

DONKPEGAN, A. S. L. 2017. Histoire évolutive du complexe Afzelia Smith (Leguminosae - Caesalpinioideae) dans les écosystèmes forestiers et savanicoles en Afrique tropicale. PhD Thesis. Université de Liège, Liège, Belgique.

DONOGHUE, M. J. 2008. A phylogenetic perspective on the distribution of plant diversity. Proc. Natl. Acad. Sci. 105: 11549–11555.

DONOGHUE, M. J., and E. J. EDWARDS. 2014. Biome Shifts and Niche Evolution in Plants. Annu. Rev. Ecol. Evol. Syst. 45: 547–572.

DOUCET, J.-L. 2003. L’alliance délicate de la gestion forestière et de la biodiversité dans les forêts du centre du Gabon. Faculté universitaire des Sciences agronomiques de Gembloux, Gembloux, Belgique.

DOUCET, J.-L., K. DAÏNOU, G. LIGOT, D.-Y. OUÉDRAOGO, N. BOURLAND, S. E. WARD, P. TEKAM, P. LAGOUTE, and A. FAYOLLE. 2016. Enrichment of Central African logged forests with high-value tree species: testing a new approach to regenerating degraded forests. Int. J. Biodivers. Sci. Ecosyst. Serv. Manag. 12: 83–95.

DRANSFIELD, J., and N. W. UHL. 2008. Genera palmarum: the evolution and classification of palms.

DROISSART, V., G. DAUBY, O. J. HARDY, V. DEBLAUWE, D. J. HARRIS, S. JANSSENS, B. A. MACKINDER, A. BLACH-OVERGAARD, B. SONKÉ, M. S. M. SOSEF, T. STÉVART, J.-C. SVENNING, J. J. WIERINGA, and T.

L. P. COUVREUR. 2018. Beyond trees: Biogeographical regionalization of tropical Africa. J. Biogeogr. 45: 1153–1167.

DUMINIL, J., R. P. BROWN, E.-E. B. EWÉDJÈ, P. MARDULYN, J.-L. DOUCET, and O. J. HARDY. 2013. Large-scale pattern of genetic differentiation within African rainforest trees: insights on the roles of ecological gradients and past climate changes on the evolution of Erythrophleum spp (Fabaceae). BMC Evol. Biol. 13: 1–13.

DUMINIL, J., M. HEUERTZ, J.-L. DOUCET, N. BOURLAND, C. CRUAUD, F. GAVORY, C. DOUMENGE, M. NAVASCUÉS, and O. J. HARDY. 2010. CpDNA-based species identification and phylogeography: application to African tropical tree species. Mol. Ecol. 19: 5469–5483.

DUMINIL, J., M. HEUERTZ, and O. J. HARDY. 2010. Chloroplast DNA Polymorphism and Phylogeography of a Central African Tree Species Widespread in Mature Rainforests: Greenwayodendron suaveolens (Annonaceae). Trop. Plant Biol. 3: 4–13.

DUMINIL, J., G. K. KOFFI, G. DEBOUT, F. SEBASTIANI, G. G. VENDRAMIN, M. HEUERTZ, S. C. GONZÁLEZ-MARTÍNEZ, and O. J. HARDY. 2011. Isolation of SSR markers for two African tropical tree species, Erythrophleum suaveolens and E. ivorense (Caesalpinioideae). Am. J. Bot. 98: e106–e108.

DUMINIL, J., S. MONA, P. MARDULYN, C. DOUMENGE, F. WALMACQ, J.-L. DOUCET, and O. J. HARDY. 2015. Late Pleistocene molecular dating of past population fragmentation and demographic changes in African rain forest tree species supports the forest refuge hypothesis. J. Biogeogr. 42: 1443–1454.

DURRIEU DE MADRON, L., R. NASI, and P. DÉTIENNE. 2000. Accroissements diamétriques de quelques essences en forêt dense africaine. Bois For. Trop. 263(1): 63–74.

EDWARDS, E. J., and S. A. SMITH. 2010. Phylogenetic analyses reveal the shady history of C4 grasses. Proc. Natl. Acad. Sci. 107: 2532–2537.

ENGELBRECHT, B. M. J., L. S. COMITA, R. CONDIT, T. A. KURSAR, M. T. TYREE, B. L. TURNER, and S. P. HUBBELL. 2007. Drought sensitivity shapes species distribution patterns in tropical forests. Nature 447: 80–82.

EPILA, J., N. BAERDEMAEKER, L. L. VERGEYNST, W. H. MAES, H. BEECKMAN, and K. STEPPE. 2017. Capacitive water release and internal leaf water relocation delay drought-induced cavitation in African Maesopsis eminii. Tree Physiol. 37: 481–490.

EPILA, J., W. H. MAES, H. VERBEECK, J. VAN CAMP, J. B. L. OKULLO, and K. STEPPE. 2017. Plant measurements on African tropical Maesopsis eminii seedlings contradict pioneering water use behaviour. Environ. Exp. Bot. 135: 27–37.

EYLES, A., E. A. PINKARD, A. P. O’GRADY, D. WORLEDGE, and C. R. WARREN. 2009. Role of corticular photosynthesis following defoliation in Eucalyptus globulus. Plant Cell Environ. 32: 1004–1014.

FADEYI, S. A., O. O. FADEYI, A. A. ADEJUMO, C. OKORO, and E. L. MYLES. 2013. In vitro anticancer screening of 24 locally used Nigerian medicinal plants. BMC Complement. Altern. Med. 13: 79.

FAUSET, S., T. R. BAKER, S. L. LEWIS, T. R. FELDPAUSCH, K. AFFUM-BAFFOE, E. G. FOLI, K. C. HAMER, and M. D. SWAINE. 2012. Drought-induced shifts in the floristic and functional composition of tropical forests in Ghana. Ecol. Lett. 15: 1120–1129.

FAYOLLE, A. ET AL. 2018. A sharp floristic discontinuity revealed by the biogeographic regionalization of African savannas. J. Biogeogr. 0.

FAYOLLE, A., D.-Y. OUÉDRAOGO, G. LIGOT, K. DAÏNOU, N. BOURLAND, P. TEKAM, and J.-L. DOUCET. 2015. Differential Performance between Two Timber Species in Forest Logging Gaps and in Plantations in Central Africa. Forests 6: 380–394.

FAYOLLE, A., J. RONDEUX, J.-L. DOUCET, G. ERNST, C. BOUISSOU, S. QUEVAUVILLERS, N. BOURLAND, F. FETEKE, and P. LEJEUNE. 2013. Réviser les tarifs de cubage pour mieux gérer les forêts du Cameroun. Bois For. Trop. 317: 36–49.

FAYOLLE, A., M. D. SWAINE, J.-F. BASTIN, N. BOURLAND, J. A. COMISKEY, G. DAUBY, J.-L. DOUCET, J.-F. GILLET, S. GOURLET-FLEURY, O. J. HARDY, B. KIRUNDA, F. N. KOUAMÉ, and A. J. PLUMPTRE. 2014. Patterns of tree species composition across tropical African forests. J. Biogeogr. 1–12.

FRIEDL, M. A., D. SULLA-MENASHE, B. TAN, A. SCHNEIDER, N. RAMANKUTTY, A. SIBLEY, and X. HUANG. 2010. MODIS Collection 5 global land cover: Algorithm refinements and characterization of new datasets. Remote Sens. Environ. 114: 168–182.

GAVIRIA, J., and B. M. J. ENGELBRECHT. 2015. Effects of Drought, Pest Pressure and Light Availability on Seedling Establishment and Growth: Their Role for Distribution of Tree Species across a Tropical Rainfall Gradient. PLOS ONE 10: e0143955.

GAVIRIA, J., B. L. TURNER, and B. M. J. ENGELBRECHT. 2017. Drivers of tree species distribution across a tropical rainfall gradient. Ecosphere 8: e01712.

GERDAT. 1977. Fiches techniques : Tali. Bois For. Trop. 17–31.

GERZ, M., C. G. BUENO, W. A. OZINGA, M. ZOBEL, and M. MOORA. 2018. Niche differentiation and expansion of plant species are associated with mycorrhizal symbiosis. J. Ecol. 106: 254–264.

GLEASON, S. M. ET AL. 2016. Weak tradeoff between xylem safety and xylem-specific hydraulic efficiency across the world's woody plant species. New Phytol. 209: 123–136.

GOETZE, D., B. HORSCH, and S. POREMBSKI. 2006. Dynamics of forest-savanna mosaics in north-eastern Ivory Coast from 1954 to 2002. J. Biogeogr. 33: 653–664.

GONMADJE, C. F., C. DOUMENGE, T. C. H. SUNDERLAND, M. P. B. BALINGA, and B. SONKÉ. 2012. Analyse phytogéographique des forêts d'Afrique Centrale: le cas du massif de Ngovayang (Cameroun). Plant Ecol. Evol. 145: 152–164.

GOREL, A., K. STEPPE, H. BEECKMAN, N. J. F. DE BAERDEMAEKER, J. DOUCET, G. LIGOT, K. DAÏNOU, and A. FAYOLLE. 2019. Testing the divergent adaptation of two congeneric tree species on a rainfall gradient using eco-physio-morphological traits. Biotropica btp.12646.

GOREL, A.-P., J. DUMINIL, J.-L. DOUCET, and A. FAYOLLE. 2019. Ecological niche divergence associated with species and populations differentiation in Erythrophleum (Fabaceae, Caesalpinioideae). Plant Ecol. Evol. 152: 41–52.

GOREL, A.-P., A. FAYOLLE, and J.-L. DOUCET. 2015. Écologie et gestion des espèces multi-usages du genre Erythrophleum (Fabaceae-Caesalpinioideae) en Afrique (synthèse bibliographique). Biotechnol Agron Soc Env. 415–429.

GRAHAM, C. H., S. R. RON, J. C. SANTOS, C. J. SCHNEIDER, and C. MORITZ. 2004. Integrating phylogenetics and environmental niche models to explore speciation mechanisms in dendrobatid frogs. Evolution 58: 1781–1793.

GUISAN, A., and W. THUILLER. 2005. Predicting species distribution: offering more than simple habitat models. Ecol. Lett. 8: 993–1009.

HACKE, U. G., J. S. SPERRY, W. T. POCKMAN, S. D. DAVIS, and K. A. MCCULLOH. 2001. Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. Oecologia 126: 457–461.

HANLEY, J. A., and B. J. MCNEIL. 1982. The meaning and use of the area under a receiver operating characteristic (ROC) curve. Radiology 143: 29–36.

HARDY, O. J., C. BORN, K. BUDDE, K. DAÏNOU, G. DAUBY, J. DUMINIL, E.-E. B. K. EWÉDJÉ, C. GOMEZ, M. HEUERTZ, G. K. KOFFI, A. J. LOWE, C. MICHENEAU, D. NDIADE-BOUROBOU, R. PIÑEIRO, and V. PONCET. 2013. Comparative phylogeography of African rain forest trees: A review of genetic signatures of vegetation history in the Guineo-Congolian region. Comptes Rendus Geosci. 345: 284–296.

HAWTHORNE, W. D. 1995. Ecological profiles of Ghanaian forest trees. University of Oxford, Oxford Forestry Institute, Department of Plant Sciences, Oxford, United Kingdom.

HEIBL, C., and C. CALENGE. 2011. phyloclim: Integrating phylogenetics and climatic niche modelling. R Package Accessed Sept.-20–2010.

HENRY, M., A. BOMBELLI, C. TROTTA, A. ALESSANDRINI, L. BIRIGAZZI, G. SOLA, G. VIEILLEDENT, P. SANTENOISE, F. LONGUETAUD, R. VALENTINI, N. PICARD, and L. SAINT-ANDRÉ. 2013. GlobAllomeTree: international platform for tree allometric equations to support volume, biomass and carbon assessment. IForest - Biogeosciences For. 6: 326–330.

HÉRAULT, B., B. BACHELOT, L. POORTER, V. ROSSI, F. BONGERS, J. CHAVE, C. E. T. PAINE, F. WAGNER, and C. BARALOTO. 2011. Functional traits shape ontogenetic growth trajectories of rain forest tree species: Plant traits shape growth trajectory. J. Ecol. 99: 1431–1440.

HIGGINS, S. I., R. BUITENWERF, and G. R. MONCRIEFF. 2016. Defining functional biomes and monitoring their change globally. Glob. Change Biol. 22: 3583–3593.

HIJMANS, R. J., S. E. CAMERON, J. L. PARRA, P. G. JONES, and A. JARVIS. 2005. Very high resolution interpolated climate surfaces for global land areas. Int. J. Climatol. 25: 1965–1978.

HOFFMANN, W. A., and A. C. FRANCO. 2008. The importance of evolutionary history in studies of plant physiological ecology: examples from cerrados and forests of central Brazil. Braz. J. Plant Physiol. 20: 247–256.

HOFFMANN, W. A., B. ORTHEN, and P. K. V. DO NASCIMENTO. 2003. Comparative fire ecology of tropical savanna and forest trees. Funct. Ecol. 17: 720–726.

HOLDO, R. M. 2006. Tree growth in an African woodland savanna affected by disturbance. J. Veg. Sci. 17: 369–378.

HOLDRIDGE, L. R. 1947. Determination of world plant formations from simple climatic data. Science 105: 367–368.

HOLSTEIN, N., and S. S. RENNER. 2011. A dated phylogeny and collection records reveal repeated biome shifts in the African genus Coccinia(Cucurbitaceae). BMC Evol. Biol. 11: 28.

HUTCHINSON, G. E. 1978. An introduction to population ecology. Available at: http://www.popline.org/node/442936 [Accessed September 14, 2017].

ITTO, 2012. Examen annuel et évaluation de la situation mondiale des bois. Yokohama, Japon : Organisation Internationale des Bois Tropicaux. Palmer E. & Pitman N., 1972. *Trees*

JETZ, W., C. H. SEKERCIOGLU, and J. E. WATSON. 2008. Ecological correlates and conservation implications of overestimating species geographic ranges. Conserv. Biol. 22: 110–119.

JOHNSON, T. C., J. P. WERNE, E. T. BROWN, A. ABBOTT, M. BERKE, B. A. STEINMAN, J. HALBUR, S. CONTRERAS, S. GROSSHUESCH, A. DEINO, C. A. SCHOLZ, R. P. LYONS, S. SCHOUTEN, and J. S. S. DAMSTÉ. 2016. A progressively wetter climate in southern East Africa over the past 1.3 million years. Nature 537: 220–224.

JONES, A., B.-M. H, B. M, D. A, J. DECKERS, D. O, G. T, H. S, J. R, K. M, L. R. P, M. E, M. L, S. O, T. L, V. R. E, Y. M, and R. B. ZOUGMORÉ. 2013. Soil Atlas of Africa. European Commission.

KATTGE, J. ET AL. 2011. TRY – a global database of plant traits. Glob. Change Biol. 17: 2905–2935.

KISSLING, W. D., W. L. EISERHARDT, W. J. BAKER, F. BORCHSENIUS, T. L. P. COUVREUR, H. BALSLEV, and J.-C. SVENNING. 2012. Cenozoic imprints on the phylogenetic structure of palm species assemblages worldwide. Proc. Natl. Acad. Sci. 109: 7379–7384.

KLEIN, T. 2014. The variability of stomatal sensitivity to leaf water potential across tree species indicates a continuum between isohydric and anisohydric behaviours. Funct. Ecol. 28: 1313–1320.

KLEIN, T. 2015. Drought-induced tree mortality: from discrete observations to comprehensive research. Tree Physiol. 35: 225–228.

KONE, I., and J. LAMBERT. 2008. Primate seed dispersal and its potential role in maintaining useful tree species in the Taï region, Côte-d’Ivoire: implications for the conservation of forest fragment. Trop. Conserv. Sci. 1: 163–306.

KÖPPEN, W. 1900. Versuch einer Klassifikation der Klimate, vorzugsweise nach ihren Beziehungen zur Pflanzenwelt. Geogr. Z. 6: 593–611.

KÖRNER, C. 2019. No need for pipes when the well is dry—a comment on hydraulic failure in trees. Tree Physiol. 39: 695–700.

KOUADIO, Y. L. 2009. Mesures sylvicoles en vue d’améliorer la gestion des populations d’essences forestieres commerciales de l’Est du Cameroun. Faculté Universitaire des Sciences agronomiques de Gembloux, Gembloux, Belgique.

KOUMBA ZAOU, P., S. NZE NGUEMA, D. MAPAGA, and P. DELEPORTE. 1998. Croissance de 13 essences de bois d’œuvre plantées en forêt gabonaise. Bois For. Trop. 21–33.

KUNZ, B. K., and K. E. LINSENMAIR. 2008. The role of the olive baboon (Papio anubis, Cercopithecidae) as seed disperser in a savanna-forest mosaic of West Africa. J. Trop. Ecol. 24: 235–246.

KYALANGALILWA, B., J. S. BOATWRIGHT, B. H. DARU, O. MAURIN, and M. VAN DER BANK. 2013. Phylogenetic position and revised classification of Acacia s.l. (Fabaceae: Mimosoideae) in Africa, including new combinations in Vachellia and Senegalia. Bot. J. Linn. Soc. 172: 500–523.

DE LA MENSBRUGE, G. 1966. La germination et les plantules des essences arborées de la forêt dense humide de la Côte d’Ivoire. Centre technique forestier tropical, Nogent Sur Marne, France.

LACHENBRUCH, B., and K. A. MCCULLOH. 2014. Traits, properties, and performance: how woody plants combine hydraulic and mechanical functions in a cell, tissue, or whole plant. New Phytol. 204: 747–764.

LACHENBRUCH, B., J. R. MOORE, and R. EVANS. 2011. Radial Variation in Wood Structure and Function in Woody Plants, and Hypotheses for Its Occurrence. In F. C. Meinzer, B. Lachenbruch, and T. E. Dawson (Eds.) Size- and Age-Related Changes in Tree Structure and Function. Tree Physiology. pp. 121–164, Springer Netherlands.

LARTER, M., S. PFAUTSCH, J.-C. DOMEC, S. TRUEBA, N. NAGALINGUM, and S. DELZON. 2017. Aridity drove the evolution of extreme embolism resistance and the radiation of conifer genus Callitris. New Phytol. 215: 97–112.

LAWTON, R. M. 1978. A Study of the Dynamic Ecology of Zambian Vegetation. J. Ecol. 66: 175.

LEBRUN, J. 1936. Répartition de la forêt équatoriale et des formations végétales limitrophes. Imprimerie industrielle et financière (Société anonyme).

LEHMANN, C. E. R. ET AL. 2014. Savanna Vegetation-Fire-Climate Relationships Differ Among Continents. Science 343: 548–552.

LENS, F., J. S. SPERRY, M. A. CHRISTMAN, B. CHOAT, D. RABAEY, and S. JANSEN. 2011. Testing hypotheses that link wood anatomy to cavitation resistance and hydraulic conductivity in the genus Acer. New Phytol. 190: 709–723.

LETOUZEY, R. 1985. Notice de la carte phytogéographique du Cameroun au 1: 500’000.

LÉZINE, A.-M., K. IZUMI, M. KAGEYAMA, and G. ACHOUNDONG. 2019. A 90,000-year record of Afromontane forest responses to climate change. Science 363: 177–181.

LI, S., F. LENS, S. ESPINO, Z. KARIMI, M. KLEPSCH, H. J. SCHENK, M. SCHMITT, B. SCHULDT, and S. JANSEN. 2016. Intervessel pit membrane thickness as a key determinant of embolism resistance in angiosperm xylem. IAWA J. 37: 152–171.

LI, X., C. J. BLACKMAN, J. M. R. PETERS, B. CHOAT, P. D. RYMER, B. E. MEDLYN, and D. T. TISSUE. 2019. More than iso/anisohydry: Hydroscapes integrate plant water use and drought tolerance traits in 10 eucalypt species from contrasting climates. Funct. Ecol. 0.

LIDDY, H. M., S. J. FEAKINS, and J. E. TIERNEY. 2016. Cooling and drying in northeast Africa across the Pliocene. Earth Planet. Sci. Lett. 449: 430–438.

LINDER, H. P. 2001. Plant diversity and endemism in sub-Saharan tropical Africa: African phytogeography. J. Biogeogr. 28: 169–182.

LINDER, H. P. 2014. The evolution of African plant diversity. Front. Ecol. Evol. 2: 38.

LINDER, H. P., H. M. DE KLERK, J. BORN, N. D. BURGESS, J. FJELDSÅ, and C. RAHBEK. 2012. The partitioning of Africa: statistically defined biogeographical regions in sub-Saharan Africa. J. Biogeogr. 39: 1189–1205.

LINDER, H. P., J. LOVETT, J. M. MUTKE, W. BARTHLOTT, N. JÜRGENS, T. REBELO, and W. KÜPER. 2005. A numerical re-evaluation of the sub-Saharan phytochoria of mainland Africa. Biol. Skr. 55: 229–252.

LOVETT, J. C., and I. FRIIS. 1996. Patterns of endemism in the woody flora of north-east and east Africa. In L. J. G. van der Maesen, X. M. van der Burgt, and J. M. van Medenbach de Rooy (Eds.) The Biodiversity of African Plants: Proceedings XIVth AETFAT Congress 22–27 August 1994, Wageningen, The Netherlands. pp. 582–601, Springer Netherlands, Dordrecht.

MAHARJAN, S. K., L. POORTER, M. HOLMGREN, F. BONGERS, J. J. WIERINGA, and W. D. HAWTHORNE. 2011. Plant Functional Traits and the Distribution of West African Rain Forest Trees along the Rainfall Gradient. Biotropica 43: 552–561.

MALEY, J. 1996. The African rain forest-main characteristics of changes in vegetation and climate from the Upper Cretaceous to the Quaternary. Proc.-R. Soc. Edinb. 104: 31–74.

MARKESTEIJN, L., and L. POORTER. 2009. Seedling root morphology and biomass allocation of 62 tropical tree species in relation to drought- and shade-tolerance. J. Ecol. 97: 311–325.

MARKESTEIJN, L., L. POORTER, F. BONGERS, H. PAZ, and L. SACK. 2011. Hydraulics and life history of tropical dry forest tree species: coordination of species' drought and shade tolerance. New Phytol. 191: 480–495.

MARKESTEIJN, L., L. POORTER, H. PAZ, L. SACK, and F. BONGERS. 2011. Ecological differentiation in xylem cavitation resistance is associated with stem and leaf structural traits: Vulnerability to cavitation of tropical dry forest tree species. Plant Cell Environ. 34: 137–148.

MARTINEZ-VILALTA, J., W. R. L. ANDEREGG, G. SAPES, and A. SALA. 2019. Greater focus on water pools may improve our ability to understand and anticipate drought-induced mortality in plants. New Phytol. 223: 22–32.

MARTÍNEZ-VILALTA, J., M. MENCUCCINI, X. ÁLVAREZ, J. CAMACHO, L. LOEPFE, and J. PIÑOL. 2012. Spatial distribution and packing of xylem conduits. Am. J. Bot. 99: 1189–1196.

MARTÍNEZ-VILALTA, J., R. POYATOS, D. AGUADÉ, J. RETANA, and M. MENCUCCINI. 2014. A new look at water transport regulation in plants. New Phytol. 204: 105–115.

MARTIN-STPAUL, N., S. DELZON, and H. COCHARD. 2017. Plant resistance to drought depends on timely stomatal closure H. Maherali (Ed.). Ecol. Lett. 20: 1437–1447.

MAYR, E., and R. J. O'HARA. 1986. The Biogeographic Evidence Supporting the Pleistocene Forest Refuge Hypothesis. Evolution 40: 55–67.

MCCULLOH KATHERINE A., JOHNSON DANIEL M., MEINZER FREDERICK C., and WOODRUFF DAVID R. 2013. The dynamic pipeline: hydraulic capacitance and xylem hydraulic safety in four tall conifer species. Plant Cell Environ. 37: 1171–1183.

MCDOWELL, N., W. T. POCKMAN, C. D. ALLEN, D. D. BRESHEARS, N. COBB, T. KOLB, J. PLAUT, J. SPERRY, A. WEST, D. G. WILLIAMS, and E. A. YEPEZ. 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? New Phytol. 178: 719–739.

MEDIAVILLA, S., and A. ESCUDERO. 2004. Stomatal responses to drought of mature trees and seedlings of two co-occurring Mediterranean oaks. For. Ecol. Manag. 187: 281–294.

MEINZER, F. C., P. I. CAMPANELLO, J.-C. DOMEC, M. G. GATTI, G. GOLDSTEIN, R. VILLALOBOS-VEGA, and D. R. WOODRUFF. 2008. Constraints on physiological function associated with branch architecture and wood density in tropical forest trees. Tree Physiol. 28: 1609–1617.

MEINZER, F. C., S. A. JAMES, and G. GOLDSTEIN. 2004. Dynamics of transpiration, sap flow and use of stored water in tropical forest canopy trees. Tree Physiol. 24: 901–909.

MEINZER, F. C., S. A. JAMES, G. GOLDSTEIN, and D. WOODRUFF. 2003. Whole-tree water transport scales with sapwood capacitance in tropical forest canopy trees. Plant Cell Environ. 26: 1147–1155.

MEINZER, F. C., B. LACHENBRUCH, and T. E. DAWSON. 2011. Size- and Age-Related Changes in Tree Structure and Function. Springer Science & Business Media.

MOLES, A. T., and M. WESTOBY. 2006. Seed size and plant strategy across the whole life cycle. Oikos 113: 91–105.

MOLL, E. J. 1977. The vegetation of Maputaland: a preliminary report on the plant communities and their present and future conservation status. Trees South Afr. 31–58.

MONCRIEFF, G. R., T. HICKLER, and S. I. HIGGINS. 2015. Intercontinental divergence in the climate envelope of major plant biomes: Intercontinental biome divergence. Glob. Ecol. Biogeogr. 24: 324–334.

MORRIS, H., and S. JANSEN. 2016. Secondary xylem parenchyma–from classical terminology to functional traits. IAWA J 37: 1–13.

MUCINA, L. 2019. Biome: evolution of a crucial ecological and biogeographical concept. New Phytol. 222: 97–114.

MUGGEO, V. 2008. Segmented: An R Package to Fit Regression Models With Broken-Line Relationships. R News 8: 20–25.

MUSCARELLA, R., P. J. GALANTE, M. SOLEY-GUARDIA, R. A. BORIA, J. M. KASS, M. URIARTE, and R. P. ANDERSON. 2014. ENMeval: An R package for conducting spatially independent evaluations and estimating optimal model complexity for Maxent ecological niche models. Methods Ecol. Evol. 5: 1198–1205.

MYERS, J. A., and K. KITAJIMA. 2007. Carbohydrate storage enhances seedling shade and stress tolerance in a neotropical forest. J. Ecol. 95: 383–395.

NAKAZATO, T., D. L. WARREN, and L. C. MOYLE. 2010. Ecological and geographic modes of species divergence in wild tomatoes. Am. J. Bot. 97: 680–693.

NEJI, M., A. GOREL, D. I. OJEDA, J. DUMINIL, C. KASTALLY, K. STEPPE, A. FAYOLLE, and O. J. HARDY. 2019. Comparative analysis of two sister *Erythrophleum* species (Leguminosae) reveal contrasting transcriptome-wide responses to early drought stress. Gene 694: 50–62.

NETSHILUVHI, T. R. 1999. Demand, propagation and seedling establishment of selected medicinal trees. South Afr. J. Bot. 65: 331–338.

NGOMANDA, A., K. NEUMANN, A. SCHWEIZER, and J. MALEY. 2009. Seasonality change and the third millennium BP rainforest crisis in southern Cameroon (Central Africa). Quat. Res. 71: 307–318.

NOSIL, P. 2012. Ecological Speciation. Oxford University Press.

O'BRIEN, M. J., B. M. J. ENGELBRECHT, J. JOSWIG, G. PEREYRA, B. SCHULDT, S. JANSEN, J. KATTGE, S. M. LANDHÄUSSER, S. R. LEVICK, Y. PREISLER, P. VÄÄNÄNEN, and C. MACINNIS-NG. 2017. A synthesis of tree functional traits related to drought-induced mortality in forests across climatic zones. J. Appl. Ecol. 54: 1669–1686.

OLIVA CARRASCO, L., S. J. BUCCI, D. DI FRANCESCANTONIO, O. A. LEZCANO, P. I. CAMPANELLO, F. G. SCHOLZ, S. RODRÍGUEZ, N. MADANES, P. M. CRISTIANO, G.-Y. HAO, N. M. HOLBROOK, and G. GOLDSTEIN. 2015. Water storage dynamics in the main stem of subtropical tree species differing in wood density, growth rate and life history traits. Tree Physiol. 35: 354–365.

OLSON, D. M., E. DINERSTEIN, E. D. WIKRAMANAYAKE, N. D. BURGESS, G. V. N. POWELL, E. C. UNDERWOOD, J. A. D'AMICO, I. ITOUA, H. E. STRAND, J. C. MORRISON, C. J. LOUCKS, T. F. ALLNUTT, T. H. RICKETTS, Y. KURA, J. F. LAMOREUX, W. W. WETTENGEL, P. HEDAO, and K. R. KASSEM. 2001. Terrestrial Ecoregions of the World: A New Map of Life on EarthA new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. BioScience 51: 933–938.

OUÉDRAOGO, D.-Y., A. FAYOLLE, S. GOURLET-FLEURY, F. MORTIER, V. FREYCON, N. FAUVET, S. RABAUD, G. CORNU, F. BÉNÉDET, J.-F. GILLET, R. OSLISLY, J.-L. DOUCET, P. LEJEUNE, and C. FAVIER. 2016. The determinants of tropical forest deciduousness: disentangling the effects of rainfall and geology in central Africa W. Cornwell (Ed.). J. Ecol. 104: 924–935.

OVERPECK, J. T., T. WEBB, and I. C. PRENTICE. 1985. Quantitative Interpretation of Fossil Pollen Spectra: Dissimilarity Coefficients and the Method of Modern Analogs. Quat. Res. 23: 87–108.

PACHAURI, R. K., L. MAYER, and IPCC eds. 2015. Climate change 2014: synthesis report. Intergovernmental Panel on Climate Change, Geneva, Switzerland.

PALMER, E., and N. PITMAN. 1972. Trees of Southern Africa, covering all known indigenous species in the Republic of South Africa, South-West Africa, Botswana, Lesotho & Swaziland. A. A. Balkema, Cape Town, South Africa.

PARMENTIER, I. ET AL. 2011. Predicting alpha diversity of African rain forests: models based on climate and satellite-derived data do not perform better than a purely spatial model: Modelling tree alpha diversity of African rain forests. J. Biogeogr. 38: 1164–1176.

PEARMAN, P. B., A. GUISAN, O. BROENNIMANN, and C. F. RANDIN. 2008. Niche dynamics in space and time. Trends Ecol. Evol. 23: 149–158.

PETERSON, A. T. 2011. Ecological niche conservatism: a time-structured review of evidence. J. Biogeogr. 38: 817–827.

PFANZ, H. 2008. Bark photosynthesis. Trees 22: 137–138.

PFAUTSCH, S., M. HARBUSCH, A. WESOLOWSKI, R. SMITH, C. MACFARLANE, M. G. TJOELKER, P. B. REICH, and M. A. ADAMS. 2016. Climate determines vascular traits in the ecologically diverse genus Eucalyptus. Ecol. Lett. 19: 240–248.

PHILIPPON, N., G. CORNU, L. MONTEIL, V. GOND, V. MORON, J. PERGAUD, G. SÈZE, S. BIGOT, P. CAMBERLIN, C. DOUMENGE, A. FAYOLLE, and A. NGOMANDA. 2018. The light-deficient climates of Western Central African evergreen forests. Environ. Res. Lett.

PHILLIPS, N. G., R. OREN, J. LICATA, and S. LINDER. 2004. Time series diagnosis of tree hydraulic characteristics. Tree Physiol. 24: 879–890.

PHILLIPS, S. J., R. P. ANDERSON, and R. E. SCHAPIRE. 2006. Maximum entropy modeling of species geographic distributions. Ecol. Model. 190: 231–259.

PINHEIRO, J., D. BATES, S. DEBROY, D. SARKAR, and R CORE TEAM. 2017. {nlme}: Linear and Nonlinear Mixed Effects Models. Available at: https://CRAN.R-project.org/package=nlme.

PITTERMANN, J., S. A. STUART, T. E. DAWSON, and A. MOREAU. 2012. Cenozoic climate change shaped the evolutionary ecophysiology of the Cupressaceae conifers. Proc. Natl. Acad. Sci. 109: 9647–9652.

PIVOVAROFF, A. L., S. C. PASQUINI, M. E. DE GUZMAN, K. P. ALSTAD, J. S. STEMKE, and L. S. SANTIAGO. 2016. Multiple strategies for drought survival among woody plant species K. Field (Ed.). Funct. Ecol. 30: 517–526.

PLANA, V. 2004. Mechanisms and tempo of evolution in the African Guineo–Congolian rainforest. Philos. Trans. R. Soc. B Biol. Sci. 359: 1585–1594.

POLLEY, H. W., C. R. TISCHLER, H. B. JOHNSON, and J. D. DERNER. 2002. Growth rate and survivorship of drought: CO2 effects on the presumed tradeoff in seedlings of five woody legumes. Tree Physiol. 22: 383–391.

POOLEY, E. 1993. The Complete Field Guide to Trees of Natal, Zululand & Transkei. Natal Flora Publications Trust, Johannesburg, South Africa.

POORTER, L. 2004. Biodiversity of West African forests: an ecological atlas of woody plant species. CABI, Wallingford, United Kingdom.

POORTER, L., and K. KITAJIMA. 2007. Carbohydrate storage and light requirements of tropical moist and dry forest tree species. Ecology 88: 1000–1011.

POORTER, L., and L. MARKESTEIJN. 2008. Seedling Traits Determine Drought Tolerance of Tropical Tree Species. Biotropica 40: 321–331.

POULSEN, J. R., C. J. CLARK, and T. B. SMITH. 2001. Seed dispersal by a diurnal primate community in the Dja Reserve, Cameroon. J. Trop. Ecol. 17: 787–808.

RATNAM, J., W. J. BOND, R. J. FENSHAM, W. A. HOFFMANN, S. ARCHIBALD, C. E. R. LEHMANN, M. T. ANDERSON, S. I. HIGGINS, and M. SANKARAN. 2011. When is a ‘forest’ a savanna, and why does it matter? Glob. Ecol. Biogeogr. 20: 653–660.

RATZMANN, G., F. C. MEINZER, and B. TIETJEN. 2019. Iso/Anisohydry: Still a Useful Concept. Trends Plant Sci. 24: 191–194.

REICH, P. B. 2014. The world-wide ‘fast-slow’ plant economics spectrum: a traits manifesto H. Cornelissen (Ed.). J. Ecol. 102: 275–301.

RICHER, R. A. 2008. Leaf phenology and carbon dynamics in six leguminous trees. Afr. J. Ecol. 46: 88–95.

ROLLAND, J., and N. SALAMIN. 2016. Niche width impacts vertebrate diversification. Glob. Ecol. Biogeogr. 25: 1252–1263.

RUNDELL, R. J., and T. D. PRICE. 2009. Adaptive radiation, nonadaptive radiation, ecological speciation and nonecological speciation. Trends Ecol. Evol. 24: 394–399.

RUNDLE, H. D., and P. NOSIL. 2005. Ecological speciation. Ecol. Lett. 8: 336–352.

RYAN, M. G., N. PHILLIPS, and B. J. BOND. 2006. The hydraulic limitation hypothesis revisited. Plant Cell Environ. 29: 367–381.

RYAN, M. G., and B. J. YODER. 1997. Hydraulic Limits to Tree Height and Tree Growth. BioScience 47: 235–242.

SANTIAGO, L. S., D. BONAL, M. E. DE GUZMAN, and E. ÁVILA-LOVERA. 2016. Drought Survival Strategies of Tropical Trees. In G. Goldstein and L. S. Santiago (Eds.) Tropical Tree Physiology. pp. 243–258, Springer International Publishing, Cham.

SANTIAGO, L. S., G. GOLDSTEIN, F. C. MEINZER, J. B. FISHER, K. MACHADO, D. WOODRUFF, and T. JONES. 2004. Leaf photosynthetic traits scale with hydraulic conductivity and wood density in Panamanian forest canopy trees. Oecologia 140: 543–550.

SCHIMPER, A. F. W. 1903. Plant-geography Upon a Physiological Basis... Clarendon Press.

SCHMERLER, S. B., W. L. CLEMENT, J. M. BEAULIEU, D. S. CHATELET, L. SACK, M. J. DONOGHUE, and E. J. EDWARDS. 2012. Evolution of leaf form correlates with tropical–temperate transitions in Viburnum (Adoxaceae). Proc. R. Soc. B Biol. Sci. 279: 3905–3913.

SCHOENER, T. W. 1968. The Anolis Lizards of Bimini: Resource Partitioning in a Complex Fauna. Ecology 49: 704.

SCHOLZ, A., M. KLEPSCH, Z. KARIMI, and S. JANSEN. 2013. How to quantify conduits in wood? Front. Plant Sci. 4: 56.

SCHOLZ, F. G., N. G. PHILLIPS, S. J. BUCCI, F. C. MEINZER, and G. GOLDSTEIN. 2011. Hydraulic Capacitance: Biophysics and Functional Significance of Internal Water Sources in Relation to Tree Size. In F. C. Meinzer, B. Lachenbruch, and T. E. Dawson (Eds.) Size- and Age-Related Changes in Tree Structure and Function. Tree Physiology. pp. 341–361, Springer Netherlands.

SCHWARTZ, D., H. DE FORESTA, A. MARIOTTI, J. BALESDENT, J. P. MASSIMBA, and C. GIRARDIN. 1996. Present dynamics of the savanna-forest boundary in the Congolese Mayombe: a pedological, botanical and isotopic (13C and 14C) study. Oecologia 106: 516–524.

SEGERS, A. 2018. Détermination des visiteurs floraux de trois essences ligneuses à haute valeur commerciale : Baillonella toxisperma Pierre, Afzelia bipidensis Harms et Erythrophleum suaveolens (Guill. & Perr.) Brenan. Master thesis. Gembloux Agro-bio Tech, Université de Liège, Belgique.

SEXTON, J. P., J. MONTIEL, J. E. SHAY, M. R. STEPHENS, and R. A. SLATYER. 2017. Evolution of Ecological Niche Breadth. Annu. Rev. Ecol. Evol. Syst. 48: 183–206.

SHEIL, D., A. SALIM, J. CHAVE, J. VANCLAY, and W. D. HAWTHORNE. 2006. Illumination–size relationships of 109 coexisting tropical forest tree species. J. Ecol. 94: 494–507.

SKELTON, R. P., A. G. WEST, and T. E. DAWSON. 2015. Predicting plant vulnerability to drought in biodiverse regions using functional traits. Proc. Natl. Acad. Sci. 112: 5744–5749.

SMITH, T., and M. HUSTON. 1990. A theory of the spatial and temporal dynamics of plant communities. In Progress in theoretical vegetation science. pp. 49–69, Springer.

SOBEL, J. M., G. F. CHEN, L. R. WATT, and D. W. SCHEMSKE. 2010. The Biology of Speciation. Evolution 64: 295–315.

SOSEF, M. S. M. 1994. Refuge Begonias: Taxonomy, Phylogeny, and Historical Biogeography of Begonia Sect. Loasibegonia and Sect. Scutobegonia in Relation to Glacial Rain Forest Refuges in Africa. Wageningen Agricultural University Papers, Studies in Begoniaceae 5.

SOSEF, M. S. M. ET AL. 2017. Exploring the floristic diversity of tropical Africa. BMC Biol. 15: 15.

SPERRY, J. S. 2003. Evolution of water transport and xylem structure. Int. J. Plant Sci. 164: S115–S127.

SPERRY, J. S. 2004. Coordinating stomatal and xylem functioning - an evolutionary perspective. New Phytol. 162: 568–570.

SPERRY, J. S., F. C. MEINZER, and K. A. MCCULLOH. 2008. Safety and efficiency conflicts in hydraulic architecture: scaling from tissues to trees. Plant Cell Environ. 31: 632–645.

STAVER, A. C., S. ARCHIBALD, and S. A. LEVIN. 2011. The Global Extent and Determinants of Savanna and Forest as Alternative Biome States. Science 334: 230–232.

STERCK, F., L. MARKESTEIJN, M. TOLEDO, F. SCHIEVING, and L. POORTER. 2014. Sapling performance along resource gradients drives tree species distributions within and across tropical forests. Ecology 95: 2514–2525.

SUCHEL, J. B. 1990. Les modalités du passage du régime climatique boréal au régime climatique austral dans le sud-ouest camerounais. Cah. Cent. Rech. Climatol. 13: 63–76.

SWAINE, M. D. 1996. Rainfall and Soil Fertility as Factors Limiting Forest Species Distributions in Ghana. J. Ecol. 84: 419–428.

SWAINE, M. D., J. B. HALL, and J. M. LOCK. 1976. The forest-savanna boundary in west-central Ghana. Ghana J. Sci. Ghana.

TCHOUTO, M. G. P., J. DE WILDE, W. F. DE BOER, L. J. G. VAN DER MAESEN, and A. M. CLEEF. 2009. Bio-indicator species and Central African rain forest refuges in the Campo-Ma’an area, Cameroon. Syst. Biodivers. 7: 21–31.

THERNEAU, T. M., and P. M. GRAMBSCH. 2013. Modeling survival data: extending the Cox model. Springer Science & Business Media.

TOSSO, D. F. 2018. Evolution et adaptation fonctionnelle des arbres tropicaux: le cas du genre Guibourtia Benn. PhD Thesis. Université de Liège, Liège, Belgique.

TUITE, P., and J. J. GARDINER. 1990. The miombo woodlands of central, eastern and southern Africa. Ir. For. 47: 90–107.

TYREE, M. T. 2002. Drought until death do us part: a case study of the desiccation-tolerance of a tropical moist forest seedling-tree, Licania platypus (Hemsl.) Fritsch. J. Exp. Bot. 53: 2239–2247.

TYREE, M. T., S. D. DAVIS, and H. COCHARD. 1994. Biophysical perspectives of xylem evolution: is there a tradeoff of hydraulic efficiency for vulnerability to dysfunction? IAWA J. 15: 335–360.

TYREE, M. T., B. M. J. ENGELBRECHT, G. VARGAS, and T. A. KURSAR. 2003. Desiccation Tolerance of Five Tropical Seedlings in Panama. Relationship to a Field Assessment of Drought Performance. Plant Physiol. 132: 1439–1447.

URLI, M., A. J. PORTE, H. COCHARD, Y. GUENGANT, R. BURLETT, and S. DELZON. 2013. Xylem embolism threshold for catastrophic hydraulic failure in angiosperm trees. Tree Physiol. 33: 672–683.

VANDEGEHUCHTE, M. W., J. BLOEMEN, L. L. VERGEYNST, and K. STEPPE. 2015. Woody tissue photosynthesis in trees: salve on the wounds of drought? New Phytol. 208: 998–1002.

VANZOLINI, P. E., and E. E. WILLIAMS. 1981. The vanishing refuge: a mechanism for ecogeographic speciation. Papéis Avulsos Zool. 34: 251–255.

VERGEYNST, L. L., M. DIERICK, J. A. N. BOGAERTS, V. CNUDDE, and K. STEPPE. 2015. Cavitation: a blessing in disguise? New method to establish vulnerability curves and assess hydraulic capacitance of woody tissues. Tree Physiol. 35: 400–409.

VERGEYNST, L. L., M. G. R. SAUSE, M. A. HAMSTAD, and K. STEPPE. 2015. Deciphering acoustic emission signals in drought stressed branches: the missing link between source and sensor. Front. Plant Sci. 6: 494.

VIOLLE, C., M.-L. NAVAS, D. VILE, E. KAZAKOU, C. FORTUNEL, I. HUMMEL, and E. GARNIER. 2007. Let the concept of trait be functional! Oikos 116: 882–892.

VIVIEN, J., and J. J. FAURE. 1985. Arbres des forêts denses d'Afrique Centrale. Agence de Développement et de Coopération Culturelle et Technique, Paris, France.

VOORHOEVE, A. G. 1965. Liberian high forest trees. Centre for Agricultural Publications and Documentation, Wageningen, Netherlands.

WALTER, H. 1973. Vegetation of the earth in relation to climate and the eco-physiological conditions. Veg. Earth Relat. Clim. Eco-Physiol. Cond.

WALTER, H., and S.-W. BRECKLE. 1985. Ecological Zonation of the Geobiosphere. In H. Walter and S.-W. Breckle (Eds.) Ecological Systems of the Geobiosphere: 1 Ecological Principles in Global Perspective. pp. 15–40, Springer Berlin Heidelberg, Berlin, Heidelberg.

WARREN, D. L., R. E. GLOR, and M. TURELLI. 2008. Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. Evolution 62: 2868–2883.

WARREN, D. L., and S. N. SEIFERT. 2011. Ecological niche modeling in Maxent: the importance of model complexity and the performance of model selection criteria. Ecol. Appl. 21: 335–342.

WATRIN, J., A.-M. LÉZINE, and C. HÉLY. 2009. Plant migration and plant communities at the time of the “green Sahara.” Comptes Rendus Geosci. 341: 656–670.

WESTOBY, M. 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. Plant Soil 199: 213–227.

WESTOBY, M., D. S. FALSTER, A. T. MOLES, P. A. VESK, and I. J. WRIGHT. 2002. Plant Ecological Strategies: Some Leading Dimensions of Variation between Species. Annu. Rev. Ecol. Syst. 33: 125–159.

WHEELER, J. K., J. S. SPERRY, U. G. HACKE, and N. HOANG. 2005. Inter-vessel pitting and cavitation in woody Rosaceae and other vesselled plants: a basis for a safety versus efficiency trade-off in xylem transport. Plant Cell Environ. 28: 800–812.

WHITE, F. 1978. The Taxonomy, Ecology and Chorology of African Ebenaceae I. The Guineo-Congolian Species. Bull. Jard. Bot. Natl. Belg. Bull. Van Natl. Plantentuin Van Belg. 48: 245–358.

WHITE, F. 1979. The Guineo-Congolian Region and Its Relationships to Other Phytochoria. Bull. Jard. Bot. Natl. Belg. Bull. Van Natl. Plantentuin Van Belg. 49: 11.

WHITE, F. 1983. The vegetation of Africa, a descriptive memoir to accompany the UNESCO/AETFAT/UNSO vegetation map of Africa (3 Plates, Northwestern Africa, Northeastern Africa, and Southern Africa, 1: 5,000,000) United Nations Educational, Scientific and Cultural Organization. Paris.

WHITTAKER, R. H. 1970. Communities and Ecosystems. Macmillan Company Available at: https://tamug-ir.tdl.org/handle/1969.3/27436 [Accessed March 12, 2019].

WIENS, J. J. 2004. Speciation and Ecology Revisited: Phylogenetic Niche Conservatism and the Origin of Species. Evolution 58: 193–197.

WIENS, J. J., and M. J. DONOGHUE. 2004. Historical biogeography, ecology and species richness. Trends Ecol. Evol. 19: 639–644.

WIENS, J. J., and C. H. GRAHAM. 2005. Niche Conservatism: Integrating Evolution, Ecology, and Conservation Biology. Annu. Rev. Ecol. Evol. Syst. 36: 519–539.

WILLIS K. J., BENNETT K. D., BURROUGH S. L., MACIAS-FAURIA M., and TOVAR C. 2013. Determining the response of African biota to climate change: using the past to model the future. Philos. Trans. R. Soc. B Biol. Sci. 368: 20120491.

WITTMANN, C., and H. PFANZ. 2008. Antitranspirant functions of stem periderms and their influence on corticular photosynthesis under drought stress. Trees 22: 187–196.

WOLFE, B. T. 2017. Retention of stored water enables tropical tree saplings to survive extreme drought conditions. Tree Physiol. 37: 469–480.

WOLFE, B. T., and T. A. KURSAR. 2015. Diverse patterns of stored water use among saplings in seasonally dry tropical forests. Oecologia 179: 925–936.

WOODRUFF, D. R., F. C. MEINZER, and K. A. MCCULLOH. 2016. Forest Canopy Hydraulics. In Canopy Photosynthesis: From Basics to Applications. Advances in Photosynthesis and Respiration. pp. 187–217, Springer, Dordrecht.

WRIGHT, I. J. ET AL. 2004. The worldwide leaf economics spectrum. Nature 428: 821.

WRIGHT, S. J., K. KITAJIMA, N. J. B. KRAFT, P. B. REICH, I. J. WRIGHT, D. E. BUNKER, R. CONDIT, J. W. DALLING, S. J. DAVIES, S. DÍAZ, B. M. J. ENGELBRECHT, K. E. HARMS, S. P. HUBBELL, C. O. MARKS, M. C. RUIZ-JAEN, C. M. SALVADOR, and A. E. ZANNE. 2010. Functional traits and the growth—mortality trade-off in tropical trees. Ecology 91: 3664–3674.

WYK, A. E. V. 1996. Biodiversity of the Maputaland Centre. In L. J. G. van der Maesen, X. M. van der Burgt, and J. M. van M. de Rooy (Eds.) The Biodiversity of African Plants. pp. 198–207, Springer Netherlands.

WYK, B. V., and P. V. WYK. 1997. Field Guide to Trees of Southern Africa. Struik, Durban, South Africa.

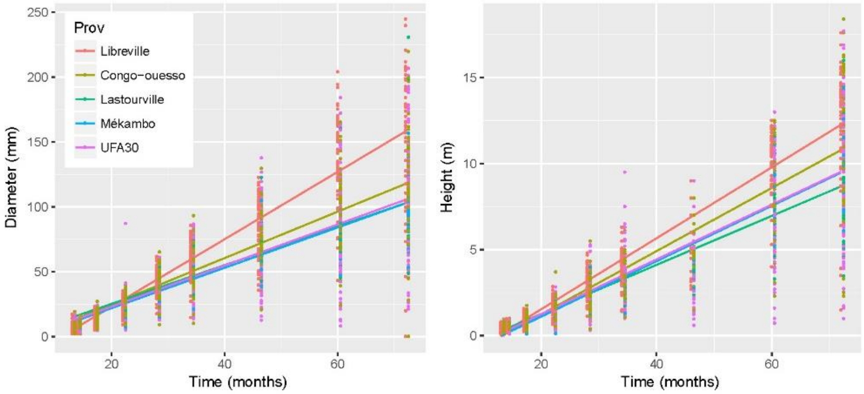
ZACHOS, J., M. PAGANI, L. SLOAN, E. THOMAS, and K. BILLUPS. 2001. Trends, Rhythms, and Aberrations in Global Climate 65 Ma to Present. Science 292: 686–693.

ZANNE, A. E. ET AL. 2014. Three keys to the radiation of angiosperms into freezing environments. Nature 506: 89–92.

ZANNE, A. E., G. LOPEZ-GONZALEZ, D. A. COOMES, J. ILIC, S. JANSEN, S. L. LEWIS, R. B. MILLER, N. G. SWENSON, M. C. WIEMANN, and J. CHAVE. 2009. Global wood density database.

ZUUR, A. F., E. N. IENO, N. J. WALKER, A. A. SAVELIEV, and G. M. SMITH. 2009. Mixed effects models and extensions in ecology with R. Gail M, Krickeberg K, Samet JM, Tsiatis A, Wong W, editors. N. Y. NY Spring Sci. Bus. Media.

Appendix



Appendix 1 Trees growth in diameter and height monitored during 8-years in a provenance trial in South-East Cameroon. One provenance (Prov) for *E. ivorense* (Libreville) and four for *E. suaveolens* (Congo-Ouesso, Lastourville, Mékambo and UFA30 (Mindourou)) have been tested. Within *E. suaveolens*, the Congo-Ouesso provenance (green) grows faster in diameter and height, but possibly at the expense of drought tolerance.