Mémoire pour le Diplôme d'Habilitation à Diriger des Recherches

Comparative ecology of tropical ecosystems (in Africa)

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Abstract

After a short presentation of my career trajectory in academia, and of the PhD students and post-doctoral fellows I had the chance to supervise, I present a synthesis of the research work I conducted over the last decade on the comparative ecology of tropical ecosystems in Africa. This work is anchored into applied forest sciences and the data that were accumulated to answer practical questions also helped answer more fundamental questions in ecology. In my work, trees are used as the starting point in the understanding of tropical ecosystems, mostly moist forests but also drier formations, such as woodlands and savannas. With a background in community and functional ecology and a position in Gembloux Agro-Bio Tech, University of Liège, targeting tropical tree allometry and forest carbon, I derived two types of comparative approaches in my research activities, I compare either sites (trees or stands) or lineages (species or genera, mostly). For the site comparison, I used either the angle of tree architecture and stand structure or that of diversity and composition, at different spatial and temporal scales, from tree allometry and biomass estimates, up to the landscape scale for the structural approach, and from diversity recovery after logging, the delineation of forest types for management and up to biogeography studies, including cross-taxonomic and cross-continent comparisons for the diversity approach. For the lineage comparison, the concept of functional traits has been central and transversal since it allowed relating the structure and diversity approaches. It was however first adapted to tropical trees for which leaves are difficult to access, and size can vary tremendously over the tree life span and among tree life histories. Allometric or size-controlled traits were notably derived from tree measurements in the field and computed at a certain diameter to compare species of contrasted morphologies. Wood anatomical traits were also investigated and notably related to tree hydraulics. In this line, I finally propose a research project on tree and forest seasonal functioning, and response to drought. Tropical forests of central Africa are indeed found under drier and more seasonal climates than their south-eastern Asian and south American counterparts, and their resilience to climate (change) is a timely topic. These research perspectives will complement ongoing work on (i) the biogeography of Africa using species occurrence derived from herbarium records instead of checklists, (ii) carbon and biodiversity changes over the last decade by re-census a set of existing plots in the Congo basin, and on (iii) the seasonality in tree and forest functioning, using tree dendrometers and phenological cameras (PhenoCams) to monitor in depth how trees cope with the dry season. This project entitled CANOPI has been accepted for founding and offer the opportunity to collect unique ground-based measurements of tree and forest functioning in central Africa.

Acknowledgements

Of course, I am grateful to a vast list of colleagues and fellows, who inspired and/or helped me to develop the research activities that are presented in this manuscript. Their name will be cited later in the document and their contributions will be detailed, but here I want to focus the attention on the fact that during this decade of exiting science on the comparative ecology of tropical ecosystems in Africa, I also had the chance to face two immense and rewarding challenges, with the birth of Juliette and Gaspard, in 2013 and 2016, respectively. The two of them have been cradled by crazy conversations about deciduousness, dissimilarities, and uncertainties during pregnancy, and both attended their first PhD or master's defence at three weeks. This would have never happened without you, Olivier. Thanks for so many things, and specifically all the things you put in the family agenda.

Nevertheless, I would like to thank Sylvie Gourlet-Fleury and Jean-Louis Doucet, for having introduced me to the tropical forests of central Africa, and for having opened the door of your research group, respectively at CIRAD and at Gembloux Agro-Bio Tech, University of Liège. I have a specific thought to Mike Swaine for the many discussions we have had and for our fruitful collaboration, and to Anaïs Gorel and Kathy Steppe, for the exiting science we have on the plate with the CANOPI project.

Table of contents

Chapter I. Curriculum vitae

I.1. General information

Adeline France Daniele

French nationality

Born in Saint-Etienne (42), France

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I.2. Academic carrer

01/04/2018 – 01/04/2020   **Director of *Forest is life***, the platform which gather the research and teaching activities of the University of Liège, not only Gembloux Agro-Bio Tech, on forest ecology and management

01/12/2017 – up to now   **Exercices and Praticals Supervisor** [Chef de travaux] at Gembloux Agro-Bio Tech, University of Liège

01/12/2012 – 31/12/2016   **Senior Teaching Assistant** [Premier assistant] at Gembloux Agro-Bio Tech, Université of Liège

15/12/2010 – 15/12/2011   **International Volunteer** detached by the French Minister for Foreign and European Affairs to the Minister of Water, Forest, Hunting, Fishing of the Central African Republic to coordinate the project for capacity building in forest research

01/04/2009 – 31/10/2010   **Post-doctoral fellow** at CIRAD, Environment and Society Department, in Montpellier, France, in the Era-Net BiodivERsA CoForChange project under the

supervision of Dr. Sylvie Gourlet-Fleury, in charge of the identification and map of forest types across the Sangha River Interval in central Africa.

01/09/2005 – 08/12/2008   **PhD student** at CNRS, Centre d'Ecologie Fonctionnelle et Evolutive in Montpellier, France, under the supervision of Dr. Eric Garnier and Pr. Marie-Laure Navas

I.3. Grants and fellowships

I have been involved several research projects in central Africa, and one project in southern Africa, though only few as Principal Investigator (PI). The projects, topics, and source of founding are detailed below.

2022 – 2025   **CANOPI** is a project funded by the EOS joint call of FNRS and FWO (~ 2 000 000 € for the whole project, 1 000 000 € for Gembloux Agro-Bio Tech, University of Liège, PI = Adeline Fayolle) for studying tropical forest resilience to climate change in Africa, in which I will coordinate two work packages, respectively on the present and future distributions of forest tree species across the African continent, and on the seasonal functioning of tropical trees and forests. The later involves combining stem growth measurements with dendrometer and crown phenology with PhenoCams.

2017 – 2022   **P3FAC** "Partenariat Public Privé pour la gestion des forêts d'Afrique Centrale" is a project funded by FFEM (CZZ 2101.01) as the second phase of the DynAfFor project (PI = Jean-Louis Doucet, 191 000 €) extending the work on forest structure, composition, and dynamics and during which I coordinated the installation and (re-)census of a set of permanent sample plots (36 ha in total) in Bambidie, Gabon (CEB logging company).

2017 – 2021   **SEOSAW** "A Socio-Ecological Observatory for Southern African Woodlands" was funded by NERC (NE/P008755/1) and allowed to assemble a vast amount of plots data across southern and eastern Africa (PI = Casey Ryan, University of Edinburgh). In this project, I provided expertise on floristic analyses and helped identify the vegetation types based on species composition.

2015 – 2017   **ACPAC** "Amélioration Continue des Plans d'Aménagement au Cameroun" was a project funded by PPEFC (~ 300 000 € for Nature+, PI = Nicolas Dubart for the project) that aimed to improve forest management rules in Cameroon. In this project, I developed the protocols and the sampling design for field measurements needed to accurately estimate stem

volumes, and with my colleague Gauthier Ligot, we also analysed the data and developed the volume equations fort the most important timber species in Cameroon.

2015 **3D-STAND** was a project funded by FNRS (~ 60 000 €, PI = Adeline Fayolle) for the acquisition of equipment (drones, cameras, and LiDAR) needed to model the 3D architecture of tropical trees.

2014 – 2018 **HERBAXYLAREDD** was a project funded by the BRAIN program of Belspo (BR/143/A3/HERBAXYLAREDD, ~ 1 000 000 € for the entire project, PI = Hans Beeckman of the Royal Museum for central Africa, and ~ 200 000 € for Gembloux Agro-Bio Tech, University of Liège, PI = Adeline Fayolle) during which I coordinated the research activities on species functional traits and distribution derived from the National Herbarium and Xylarium.

2013 – 2016 (+2 yrs) **PreREDD+** was funded by a gift of the Global Environment Fund administrated by the World Bank (TF010038) for capacity building in central Africa related to the REDD+ mechanisms (~ 1 500 000 € for the consortium ONFi/TEREA/Nature+, PI for Nature+ = Adeline Fayolle, 140 000 €). In this project, I coordinated the research activities on tree allometry (biomass), and I developed the allometric equations for the forest types of the Congo basin.

2013 – 2018 **DynAfFor** "Structure et dynamique des forêts d'Afrique centrale : vers des règles d'exploitation du bois intégrant le fonctionnement écologique des populations d'arbres et la variabilité des conditions environnementales" was a project funded by FFEM (CZZ1636.01D and CZZ1636.02D) and which aimed to develop forest management rules adapted to tree populations and environmental conditions (PI = Jean-Louis Doucet for Gembloux Agro-Bio Tech, University of Liège, ~ 300 000€). In this project, I was involved in the research activities on tree allometry (height-diameter relationships) and biomass estimation.

2012 **EBALAC** "Estimation de la Biomass Aérienne Ligneuse en Afrique Centrale" was funded by the capital stock of the research unit "Forest resource management" in Gembloux Agro-Bio Tech and benefitted from the facilities of the Pallisco-CFIM company in Cameroon. In this project, I build allometric equations (biomass) for central Africa and tested the validity of pantropical equations (~ 200 000 €, PI = Adeline Fayolle).

I also obtained the following grants.

2008 **Mobility grant** from the doctoral school SIBAGHE for a research stay at Silkeborg Denmark, collaborating with Dr. Christiand Damgaard at NERI

2005 – 2008 **PhD fellowship** from CNRS and Languedoc Region in France

I.4. Teaching activities

In Gembloux Agro-Bio Tech, University of Liège, I am involved as teacher and/or coordinator of several courses of the master on forest and nature management.

2017 – FORE0028 Group project (coord. Adeline Fayolle), Master 2, 6/6 ECTS

2015 – MATH2016 Mathematics and dynamic systems modelling (coord. Pr. Catherine Charles) Licence 3, 2h dedicated to the introduction to matrix models of population dynamics and their usefulness for forest management and biodiversity conservation

2014 – FORE004 Dendrometry and forest inventory (coord. Adeline Fayolle since 2017, with Dr. Gauthier Ligot), Master 1, 2/4 ECTS

2012 – FORE0042 News about tropical forests (coord. Pr. Jean-Louis Doucet) Master 2, 1/2 ECTS

2012 – BIOD007 Methods for biodiversity analyses (coord. Adeline Fayolle since 2021, with Dr. Arnaud Monty), Master 1, 3/6 ECTS

I was earlier involved in courses given at the University of Bangui in the Central African Republic, and at the University of Montpellier and at Montpellier SupAgro, in France, mostly practical courses in plant sciences (anatomy of Angiosperms), ecology (secondary successions) and data management and analyses (introduction to R).

I.5. Mentoring activities

I have been involved in the supervision of nine PhD fellows and four of them have successfully obtained their PhD and are still active in science. Among the five ongoing PhDs I am involved in one student is about to finish and three are quite recent (fellowships obtained in 2021). The PhD students and their research topics are listed below. The source of founding (type of fellowship) and the investment in supervision [% of mentoring] are also indicated.

2021 –2025 **Modestine Kompanyi** works on the structure and diversity, and carbon balance of the tropical forest of the Lomami, an enigmatic area of the Congo basin (FRIA fellowship) with Dr. Wannes Hubau at the University of Gent and Royal Museum for Central Africa [70%].

2021 –2025 **Pauline Depoortere** works on carbon stocks and structural components of biomass in central Africa (FNRS fellowship) with Pr. Jean-François Bastin [30%].

2021 – 2025 **Lisette Mangaza** works on the response of forest structure and diversity to degradation in DRC (4 months fellowship from PACODEL and PhD fellowship from the PRECOB project ENABEL) with Pr. Jean-Rémy Makana at the University of Kisangani [70%].

2017 – 2024 **Chloé Dupuis** works on the monitoring of forest degradation (research assistant, 3×2 years) with Pr. Philippe Lejeune [30%].

2017 – 2021/22 **Davy Fonteyn** finishes his work on mammal communities in central Africa (FRIA fellowship + 3-months extension due to COVID pandemics) with Pr. Cédric Vermeulen [70%].

2017 – 2021 **Bhély Angoboy Ilondea** (at University of Gent) worked on the phenology and growth of tropical trees in the Luki Man and Biosphere reserve in the DRC (HERBAXYLAREDD project) with Pr. Joris van Acker at the University of Gent, Dr. Hans Beeckman at the Royal Museum for Central Africa and Pr. Tom de Mil [20%].

2015 – 2020 **Simon Lhoest** addressed the relationships between biodiversity and ecosystem services in central Africa (FRIA fellowship) with Pr. Marc Dufrêne [70%].

2014 – 2018 **Grace Jopaul Loubota Panzou** worked on the allometry of tropical trees in central Africa (fellowships from the Congolian government and FISE) with Pr. Jean-Joël Loumeto at the University Marien-Ngouabi [70%].

2013 – 2019 **Anaïs Gorel** worked on the ecological specialisation within the *Erythrophleum* genus in Africa (research assistant, 3×2 years) with Pr. Jean-Louis Doucet [70%].

I have also been involved in the mentoring of several post-doctoral fellows, their name and research topics are listed below, so the source of founding (type of fellowship) and the investment in supervision [% of mentoring].

2021 – 2023 **Anaïs Gorel** works on biome transition in the woody flora of tropical Africa (BOF fellowship from the University of Gent, detached to Gembloux Agro-Bio Tech, University of Liège) with Pr. Kathy Steppe [70%].

2020 **Anaïs Gorel** worked on niche modelling and evolution within the woody flora of tropical Africa (research unit founds) [100%].

2019 – 2021   **Pedro Luis Silva de Miranda** worked on the cross-continent comparison of the richness of the woody flora in tropica Africa and South America (IPD-STEMA fellowship from the University of Liège) [100%].

2019   **Grace Jopaul Loubota Panzou** worked on crown-diameter allometric relationships (WBI out, Exeter University, UK) with Pr. Ted Feldpausch [30%].

2018   **Julie Aleman** worked on the distribution of tropical biomes in Africa (HERBAXYLAREDD project) [100%].

2018 – 2019   **Gauthier Ligot** worked on the species and forest dynamics in central Africa (DynAfFor project) with Pr. Jean-Louis Doucet [50%].

2016-2017   **Dakis-Yaoba Ouédraogo** worked on the phenology of tropical trees in Africa (HERBAXYLAREDD project) [100%].

2015   **Dakis-Yaoba Ouédraogo** worked on the tropical silviculture in Africa (research unit founds) with Pr. Jean-Louis Doucet [50%].

I.6. Reviewing and editorial work

I have served as Reviewer for many journals, and since 2018, I am **Subject Editor for African Journal of Ecology** edited by Wiley. I was recently asked by the Editor Pr. Katherine Abernethy from the University of Stirling in UK to continue and even to extend my role. I am also a member of the editorial committee of the French journal edited by CIRAD Bois et Forêts des Tropiques.

Chapter II. Dissemination

II.1. Research topics

I was hired in Gembloux Agro-Bio Tech, University of Liège, to develop research activities related to the framework created by the United Nations Framework Convention on Climate change (UNFCCC) Conference of the Parties (COP) to guide activities in the forest sector that **R**educes **E**missions from **D**eforestation and forest **D**egradation, as well as the sustainable management of forests and the conservation and enhancement of forest carbon stocks in developing countries, the **REDD+ mechanism**. Since 2012, I have developed research activities on tropical tree allometry, biomass stocks and biomass dynamics in central Africa. The latter was possible thanks to the long-term monitoring of the forest plots in M'Baïki, since 1982. Using tree and wood measurements needed for biomass estimates, I also initiated the development of size-controlled or allometric traits. Beyond structure, my research interests also encompass the variation in diversity (mostly composition), using ground plot data, so as forest and tree functioning, specifically phenology, using field observations of tree crowns, and to a lesser extent, using satellite and PhenoCam observations, and herbarium specimens. To get a deeper functional understanding of the observed patterns, wood traits and tree hydraulics were also explored on a restricted set of species. The large amount of plot data from forest inventory I used in collaboration with logging companies, and my international network, lead me to larger-scale studies of the biogeography of the African continent. Notably, I have identified floristic discontinuities in tree species composition for moist forests, and then adopted the same approach for drier formations, savannas, and woodlands, that enabled the delimitation of the main floristic units in both biomes. Then, we combined the forest and savanna datasets and provided floristic evidence for alternative biome states given the vast climatic space where both moist forest and savanna coexist across Africa. Though the floristic divergence between the forest and savanna biomes, some lineages encompass both biomes and we recently investigated the biome shifts in the evolutionary history of woody lineages in Africa, in a study just published in Ecology Letters. The biogeography approach I developed for moist forests and savannas based on species lists, was further applied for terrestrial mammals in central Africa, and we confronted our zooregions to threats (defaunation level and lack of forest integrity) and to the conservation network. Finally, with Brazilian colleagues, we established the first cross-continent comparison of the (sub)tropical woody flora of Africa and South America, confirming

the "odd man out" pattern that Africa is depauperate in a study just accepted in PNAS. The marked species richness difference between South America and Africa is due primarily to a key group of families in the Amazon and Atlantic Moist Forests, which while present and speciose in Africa, are markedly less diverse there.

II.2. Publications

In one decade, I have established myself as one of the main specialists in African tree ecology in the world, having published more than 80 scientific papers in international journals on the topic (H-index=24 on Scopus) and two book chapters. The full list of my publications is available on Google Scholar, https://scholar.google.be/citations?hl=en&user=wkaUmUQAAAAJ. The 86 documents that are referenced on Scopus have been cited 1,859 times by 1,379 documents. Specifically, I have written nine scientific articles as first author, two as co-first author, and 21 as last author with my PhD students and post-doctoral fellows as first author. My ambition is to **decolonize and feminize the scientific research** in tropical Africa and I am glad to have in my present and former PhD students and post-doc fellows a good balance between southern and northern people, and male and female.

II.3. Conferences

In my early career, I experienced difficulties to finalize (and publish) my research work, and I once decided not to present my work at conferences before it has been published. This decision, the two kids I had while working in Africa, and the two years of pandemic, explain why I have not been particularly active in presenting my work at international conferences. The following events I attended can however be mentioned.

2019/04   Participation to the **European Conference of Tropical Ecology**, Edinburgh, UK with a talk entitled "Biogeography and evolutionary ecology of the woody flora in tropical Africa"

2018/08   Participation to the 18th Meeting of the **Congo Basin Forest Partnership Parties** Scientific day in Tervuren, Belgium with a talk entitled "The fate of tropical forests across Africa: insights from the forest and savanna distributions"

2018/03   Organization of a symposium on tree allometry and biomass estimates, and participation to the **European Conference of Tropical Ecology**, Paris, France with an introductory talk for the symposium entitled "State of the art on tropical tree allometry"

2018/01   Chicheley Hall, Newport Pagnell, UK, keynote speaker at the **Theo Murphy conference** "Tropical phenology: functional change in ecosystems across space and time" with a talk entitled "Phenological strategies and trends witnessed across Africa"

2017/04   Participation to the second **consultative committee of the forest administration** in Yaoundé, Cameroon presenting the results of a pilot study on volume equations (ACPAC project)

2017/02   Organization of a symposium on functional traits and strategies, and participation to the **European Conference of Tropical Ecology** (former GTOE), Brussels, Belgium with a talk entitled "Woody species composition of African savannas and dry forests"

2015/05   Organization of a session on functional traits and participation to the **Xylaredd conference** "Wood science underpinning tropical forest ecology and management", in Tervuren, Belgium with a talk entitled "Does the rate of carbon accumulation continually increase with tree size?"

2012/09   Participation to the **phenology workshop organized by WCS** in Bwindi, Uganda

2012/11   Organization and participation to the **one-day conference on the REDD+ mechanism**, Gembloux, Belgium with a talk entitled "Are pantropical allometric equations valid for central Africa?"

I was also involved in the organization of the following events in Belgium.

2022   Organization of the **international Chaire Franqui conference cycle** by Pr. David Ellsworth on "Future climate risks to our natural capital" at Gent, but also Hasselt, Antwerp, Gembloux, Brussels, and Louvain-La-Neuve, Belgium

2019/03   Organization of the **Chaire Franqui conference cycle** by Dr. Jérôme Chave on the "Vulnerability of tropical forests to future climates" at Gembloux, Belgium

II.4. Other scientific outputs

Several practical implications have been derived from my work. Specifically, my work on tropical tree allometry has allowed defining which biomass equations to use for the estimation and monitoring of forest carbon stocks in the Congo basin (Fayolle *et al.* 2013a, 2018) and which volume equations to be used in management planning by timber companies and in controls

performed by the forest administration (Fayolle *et al.* 2013b; Ligot *et al.* 2018a). Together with my former post-doctoral fellow, Dr. Julie Aleman, we produced the most accurate map of the forest and savanna distributions in Africa (Figure 1a), which take into account differences in tree species composition, and a complex suite of determinants (Aleman *et al.* 2020). This result published in PNAS is not only important for understanding the biogeography of the continent but also, to guide large-scaled tree planting and restoration efforts planned for the region. In a paper published in Nature, and lead by Maxime Rejou-Méchain, from IRD, France, the forest types of the Congo basin were mapped for the first time (Figure 1b) and the guidelines for forest management are precisely given for each forest type (Réjou-Méchain *et al.* 2021). This work followed a decade of research in central Africa, in which management inventory by logging companies have been collated and analysed to identify and map forest types across the Sangha River Interval first (Fayolle *et al.* 2014a) and then across the entire region, with the idea that improved characterization of forest types is the first step for guiding forest management (Gourlet-Fleury *et al.* 2014). In the same line, management parameters imposed by forest administration were evaluated for several timber species, notably growth in Cameroon (Fétéké *et al.* 2015; Ligot *et al.* 2019) and the size (diameter) at reproduction across the region (Ouédraogo *et al.* 2018).
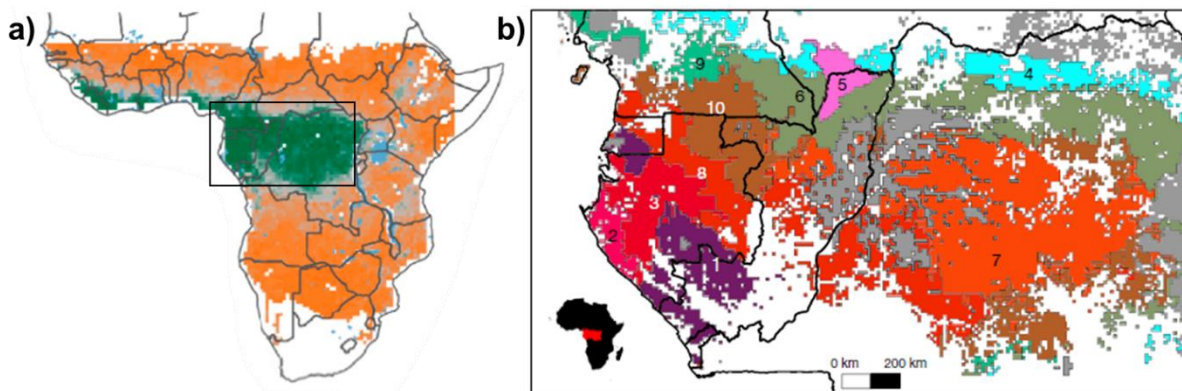
Figure 1. Vegetation maps useful for management and conservation. The distribution of the forest (in green, a) and savanna (in orange) biomes in (sub)tropical Africa is extracted from Aleman *et al.* (2020) and that of the forest types of the Congo basin (b) is extracted from Réjou-Méchain *et al.* (2021) with Atlantic highland evergreen (1), Atlantic coastal evergreen (2), Atlantic inland evergreen (3), margin semi-deciduous (4), semi-deciduous on sandstone (5), semi-deciduous (6), central evergreen (7), mixed evergreen (8), degraded semi-deciduous (9) and transition between semi-deciduous and evergreen (10).

Chapter III. Research activities

III.1. Tropical tree allometry and forest biomass

III.1.1. Initial research project

In January 2012, after an 18-months post-doc at CIRAD working with forest inventory data to delineate and map forest types in the Sangha River Interval – the area between the Lower Guinean and Congolian subcentres of endemism of the Guineo-Congolian Region of White (1983) – and a one-year experience in the Central African Republic (CAR) supervising the research activities in M'Baïki, I started a position in Gembloux Agro-Bio Tech, University of Liège. This position requested to develop research activities in forest sciences related to the implementation of the REDD+ mechanism. Given the strong focus on central Africa of the 'Tropical Forestry Laboratory' headed by Jean-Louis Doucet, I proposed a research project allowing to improve biomass estimates for the Congo basin forests and focusing on tree above-ground biomass (AGB) because the living biomass of trees is the major pool of carbon in forest ecosystems and the other pools of carbon (below-ground biomass, dead organic matter (woody debris and litter) and soil organic matter) are usually derived from AGB estimates (Aalde *et al.* 2006). I specifically proposed three research topics or axes, and **the first research axis was to develop allometric equations for central Africa**, because at the time, the biomass equations available for the region were restricted to specific species and sites (Figure 2), such as the *Eucalypt* plantations in Pointe Noire, Congo.

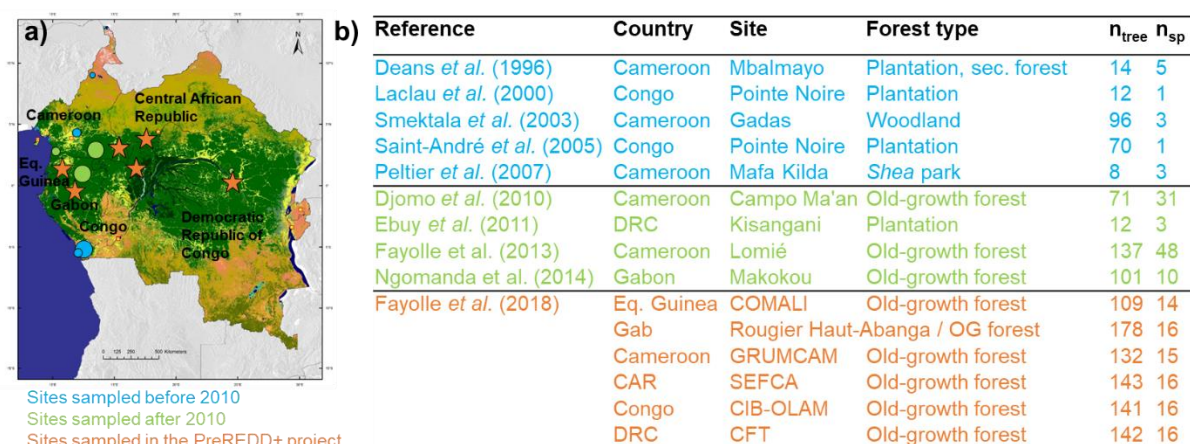| Reference	Country	Site	Forest type	n$_{tree}$	n$_{sp}$
Deans *et al.* (1996)	Cameroon	Mbalmayo	Plantation, sec. forest	14	5
Laclau *et al.* (2000)	Congo	Pointe Noire	Plantation	12	1
Smektala *et al.* (2003)	Cameroon	Gadas	Woodland	96	3
Saint-André *et al.* (2005)	Congo	Pointe Noire	Plantation	70	1
Peltier *et al.* (2007)	Cameroon	Mafa Kilda	*Shea* park	8	3
Djomo *et al.* (2010)	Cameroon	Campo Ma'an	Old-growth forest	71	31
Ebuy *et al.* (2011)	DRC	Kisangani	Plantation	12	3
Fayolle et al. (2013)	Cameroon	Lomié	Old-growth forest	137	48
Ngomanda et al. (2014)	Gabon	Makokou	Old-growth forest	101	10
Fayolle *et al.* (2018)	Eq. Guinea	COMALI	Old-growth forest	109	14
	Gab	Rougier Haut-Abanga / OG forest		178	16
	Cameroon	GRUMCAM	Old-growth forest	132	15
	CAR	SEFCA	Old-growth forest	143	16
	Congo	CIB-OLAM	Old-growth forest	141	16
	DRC	CFT	Old-growth forest	142	16

Figure 2. Availability of destructive biomass data and equations in central Africa. The location of AGB data and equations available for central Africa (a) is shown on a base ground map of vegetation types

(Verhegghen *et al.* 2012), and sampling effort according to the number of tree and species sampled is also provided for each individual study (b). The six sites later sampled in the frame of the PreREDD+ project (Fayolle *et al.* 2018) are also shown (orange stars on the map).

For the entire sub-Saharan region, the available data and equations were reviewed by Henry *et al.* (2011), and with the exception of the work of Henry *et al.* (2010) in Ghana, existing allometric equations were fitted on small datasets not fulfilling the recommendations of Chave *et al.* (2004) of more than 100 trees covering a vast range of diameter and species wood density. Given this lack of data and allometric equations for Africa, the common practice was to use the pantropical model developed by Chave *et al.* (2005) for estimating the biomass at the tree scale. Though we latter proved this model to be valid in Cameroon (Fayolle *et al.* 2013a), this model was highly criticized in central Africa, because the calibration dataset did not include any trees sampled in Africa. **The second research axis concerned forest biomass and carbon stocks**, and given my background in community and functional ecology, I proposed to link biomass, and forest structure more generally, to diversity, mostly composition (beta diversity). **The third research axis was related to the monitoring of the deforestation process**, its spatial extent and dynamics in the Congo basin using temporal data at national or regional scales. Finally, over the last decade, I only addressed the first two topics, and mostly the first one. I must admit. Several aspects of tropical tree allometry will thus be explored below.

III.1.2. Biomass and volume equations

Over the 2010–2020-decade, research efforts converged toward the estimation and monitoring of carbon stocks in forest ecosystems in order to make REDD+ a reality (Gibbs *et al.* 2007). The **estimation of carbon stocks** in tropical forests starts with tree measurements in plots installed in the field that are converted into biomass estimates at the tree level with an allometric equation (Clark & Kellner 2012). The first complete error propagation study showed that the choice of the allometric equation used to convert tree diameters (and possibly height) into above-ground biomass (AGB) estimates is the major source of uncertainty (~ 40%) in the biomass estimation process from the tree to the landscape level (Chave *et al.* 2004). This result was later confirmed by Molto *et al.* (2013) who found that the uncertainty in the AGB estimates was found to derive primarily from the AGB sub-model. AGB estimates at the tree level are then summed at the plot level and converted into carbon estimates, assuming carbon content to be 50% of tree biomass. However, recent studies indicate that this assumption is not accurate, with substantial variation among tree species as well as among tissue types (Thomas & Martin 2012). The value of 45.6% was used for tropical trees in recent studies (Hubau *et al.* 2020).

The choice of the allometric model being so important, **a renewed interest in tropical tree allometry research** was observed across the global tropics, and even more in central Africa (Figure 2) given the lack of appropriate biomass data and equations (Henry *et al.* 2011). It was first demonstrated by Vieilledent *et al.* (2012) in Madagascar that the pantropical model developed by Chave *et al.* (2005) gave accurate biomass estimates, and we obtained the same results in Cameroon (Fayolle *et al.* 2013a). While these two studies argued for the null hypothesis that the allometry of **African tree species does not differ from common allometric patterns that have been reported across the tropics**, the work of our colleagues in Gabon (Ngomanda *et al.* 2014) challenged this view. They indeed reported a systematic over-estimation of about 40% of tree AGB using the pantropical model of Chave *et al.* (2005) for moist forest (the forest type according to rainfall), while the model for wet forest provided accurate predictions. Two reasons could explain these discrepancies. The first reason is related to the approach employed in Gabon using direct weights of fresh biomass and later converted in dry biomass with the dry matter content of samples, but without any local information on wood density (Ngomanda *et al.* 2014). Wood density is however the second most important AGB predictor after tree diameter (Chave *et al.* 2005) and is even more important than the number of trees used for fitting (Van Breugel *et al.* 2011). The second reason is related to the forest types defined in Chave *et al.* (2005) who used Holdrige's life zone (1967) as in the seminal work of Brown *et al.* (1989). Indeed, the different forest types recognized and for which pantropical allometric equations were provided (Chave *et al.* 2005) were: 'wet forests' including lowland high-rainfall forests (with rainfall greater than 3,500 mm yr^{-1} and no seasonality) and montane cloud forests, 'moist forests' which are found under drier and more seasonal climates (with 1,500–3,500 mm yr^{-1} in rainfall and a dry season of one to four months) and sometimes show a semi-deciduous canopy, and 'dry forests' which are found under even much drier and more seasonal climates (with rainfall below 1,500 mm yr^{-1} and a pronounced dry season, over five months). These forest types and associated rainfall thresholds do not necessarily match with the distinction between evergreen and moist forests in Africa that have been long recognized (White 1983) but only recently mapped in collaboration with our colleagues from IRD, CIRAD and several research institutions in central Africa (Réjou-Méchain *et al.* 2021). Tropical forests in central Africa are indeed found under drier and more seasonal climates than their south American counterparts (Parmentier *et al.* 2007) and moist semi-deciduous forests cover vast areas in Africa (Fayolle *et al.* 2014a, b). Evergreen forests dominates in Gabon, under seasonal and relatively dry climate (~ 1500 mm at Lopé NP), because the cloudy dry season prevents evapotranspiration (Philippon *et al.* 2019) and allow maintaining an evergreen canopy below the 2,000 mm yr^{-1} rainfall thresholds recognized across the global tropics (Guan *et al.* 2015).

Including total tree height in the AGB predictors was nevertheless found to be more important than the forest type (Chave *et al.* 2005) and in the follow up study including trees sampled in several sites across tropical Africa (Chave *et al.* 2014) a pantropical model was retained for wet, moist and dry forests. Our destructive dataset from Cameroun (148 trees belonging to 42 species), including the heaviest tree measured at the time, a Sapelli tree (*Entandrophragma cylindricum*, Meliaceae) of 192 cm diameter and weighing 72 tons, was not included in the follow up pantropical study (Chave *et al.* 2014) because total tree height was not measured prior to felling. Data collection was already ongoing when I arrived in the group, and the team on the field did not accept to include a new measurement, total tree height, since they already measured the commercial height, *i.e.*, the height of the first deformation in the stem. This dataset was however used in a cross-site analysis showing the need to include crown information in the biomass estimation for large trees (Ploton *et al.* 2016) and in an applied study testing the validity of **volume equations** used in Cameroon for three species with sufficient sampling, Assamela (*Pericopsis elata*, Fabaceae), Sapelli and Tali (*Erythrophleum suaoveolens*, Fabaceae). In the latter study, we found that volume equations available from the neighboring countries provided accurate predictions of commercial volume, with the exception of the volume equations imposed by the forest administration in Cameroon (Fayolle *et al.* 2013b). The systematic underestimation of commercial volume by the equations imposed by the administration was known by the forest managers since they regularly encounter problems with the forest administration. Each year before the summer, the exploited volumes exceed the volume allowed to be exploited during the entire year, because the volume of standing trees is underestimated by the volume equations imposed by the forest administration. We more recently discovered that the volume of felled trees is also overestimated during controls exacerbating the problem. After this preliminary work on volume estimation using the data of the EBALAC project focusing on biomass, I participated into the ACPAC project hold by Nature+ during which updated equations were provided for most timber species exploited in Cameroon (Ligot *et al.* 2018a), and I showed myself the published results to the forest administration. Also with Nature+ we established a biomass equation for the Mampu-like agroforestry system on the Batéké plateaux in the Democratic Republic of Congo (DRC), where *Acacia auriculiformis* are planted and mixed with crops in the first years, then trees are left for ~ eight years before harvest for charcoal production (Proces *et al.* 2017).

If we move back to the estimation of biomass and carbon stocks in natural forests, before the new and general pantropical model of Chave *et al.* (2014) predicting tree AGB from species wood density, total tree height and tree diameter, **a consensus was still lacking in central Africa**. Uncertainty remained on the choice of the allometric model, because the moist and the

wet forest equations were respectively supported by the data in Cameroon (Fayolle *et al.* 2013a) and in Gabon (Ngomanda *et al.* 2014). Also with Nature+, in a consortium with two forest consultant offices, ONFi and TEREA, I was involved in a project entitled PreREDD+, during which a massive campaign of destructive biomass measurements was conducted in six sites distributed across central Africa (orange stars on Figure 2). I designed the protocol for the data collection (Figure 3) which was adapted from Fayolle *et al.* (2013a). In PreREDD+ we benefitted from our earlier experience, and we adapted the existing database for data encoding, LEEBAC, developed by Samuel Quevauvillers in Gembloux Agro-Bio Tech, University of Liège, during our first project, and which computes all calculations from field and laboratory measurements, so as stump area digitalized on georeferenced photographs (Figure 3f). In terms of sampling, we followed the strategy of Ngomanda *et al.* (2014), targeting at least ten trees for about ten abundant species in each site, and we also tried to sample a few species in several sites.
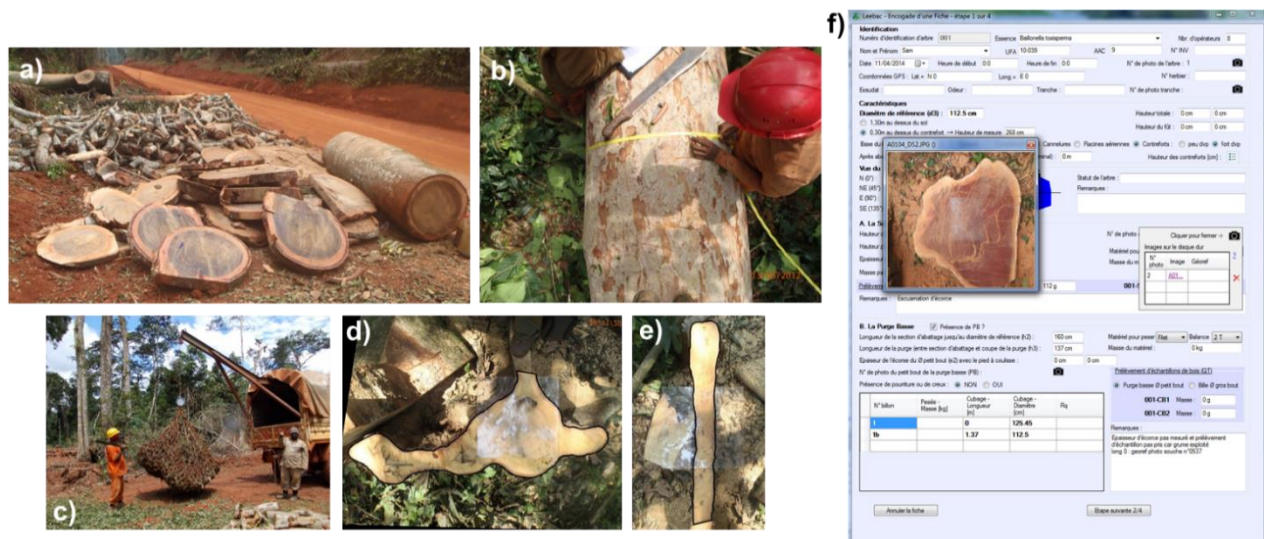

Figure 3. Destructive biomass measurements in the field and data encoding. After felling the tree is divided into compartments (a), the diameter is measured on the regular parts of the stem and branches for cubing (b), the irregular compartments such as small branches are weight (c), and in our approach photographs of the stump left in the field were made and used for digitalization of the stump area (d-e). Field and laboratory data were encoded in the LEEBAC database (f) developed by Samuel Quevauvillers.

In the PreREDD+ project, the data collection in the field was regularly controlled by Josiane Kondaoule from TEREA and by Adrien Peroches from ONFi, and I analyzed the final regional dataset (Fayolle *et al.* 2018). For the project deliverables, I tested whether central African forests are different from other tropical forests with respect to biomass allometry, and further examined the regional variation in tropical tree allometry across the Congo basin forests (Fayolle *et al.* 2018). Examining the performance of general models (pantropical or regional) *versus* local models (site-specific), I found **little advantage of using local equations and earlier pantropical equations were found to provide reasonable predictions of tree AGB** in most

sites, notably the equations developed for moist forests (Chave *et al.* 2005) and for the global tropics (Chave *et al.* 2014), though the wettest sites, *i.e.*, evergreen forests in Equatorial Guinea and, to a lesser extent in Gabon, tended to show a wet forest allometry (Figure 4). On the regional dataset, I fitted regional and local allometric models including tree diameter, wood specific gravity, tree height, and crown radius in the AGB predictors and in contrast to expectations, I found that including tree height and crown radius had a significant but very small effect on AGB predictions (Fayolle *et al.* 2018). This results indeed contrasts with the recognized importance of height-diameter allometry (Feldpausch *et al.* 2011) and that of crown information (Goodman *et al.* 2014), specifically for extremely large trees (Ploton *et al.* 2016). I do not have any explanation yet, but the role of wind needs to be further explored, as shown for height-diameter allometry (Thomas *et al.* 2015).
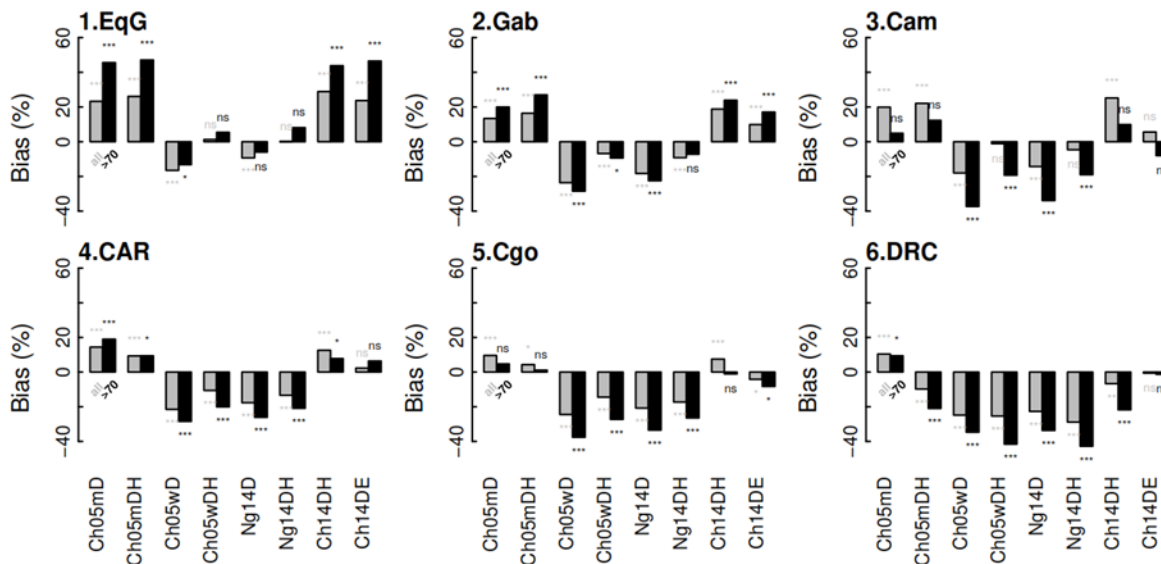

Figure 4. Prediction test of existing allometric equations on the PreREDD+ dataset. The mean value and significance of the relative bias (in %) in AGB predictions at the tree level is given for the pantropical equations developed by Chave *et al.* (2005) for moist forests (including in the predictors, wood specific gravity and tree diameter, Ch05mD, and additionally total tree height, Ch05mDH) and wet forests (including wood specific gravity and tree diameter, Ch05wD, and additionally height, Ch05wDH), and by Chave *et al.* (2014) for all tropical forests (including wood specific gravity, tree diameter, and height, Ch14DH, or the environmental stress variable, Ch14DE), and from the local equations developed by Ngomanda *et al.* (2014) in Gabon (including wood specific gravity and tree diameter, Ng14D, and additionally height, Ng14DH). Prediction tests were performed at the site level for all sampled trees (in grey) and separately for large trees (diameter > 70 cm, in black). Significance levels correspond to: *** for *P*<0.001, ** for *P*<0.01, * for *P*<0.05, and ns for not significant. Sites are ordered from West to East. Extracted from Fayolle *et al.* (2018).

The PreREDD+ dataset can be considered as **the largest ever destructive sampling for a tropical region**, with a total of 845 tropical trees sampled in six sites representative of terra firme forests and belonging to 55 African species and covering many trees (> 100) and a large

range of diameters (up to 200 cm) in each site. The dataset was also used to explore the between-species variations in wood density profiles, from the stump and up to the branches (Momo *et al.* 2020), and in biomass allometry (Mankou *et al.* 2021).

III.1.3. Height-diameter and crown allometries

Given that tree height is an important AGB predictor, at the third rank after tree diameter and species wood density (Chave *et al.* 2005), that was missing in our first biomass allometry work (Fayolle *et al.* 2013a), we investigated the **between-species and -site variation in height-diameter allometry** in Cameroon, the latter having been popularized across the tropics (Feldpausch *et al.* 2011; Banin *et al.* 2012). This work was initiated in the frame of the master's thesis of Grace Jopaul Loubota Panzou who later performed a PhD thesis in his home country the Republic of Congo. He collected height and diameter data for timber species in two sites (and logging concessions), in the Ma'an site (logging concession managed by the Wi'jma company, whose activities have been suspended since) and in the Mindourou site (logging concession managed by the Pallisco-CFIM company). During the field campaign, the student sent me the data regularly and I asked him to continue the sampling of large trees until an asymptote in total tree height was reached, which appeared around 100 cm in diameter. We first examined the **shape of the height-diameter relationships** at the site level and reviewed the models that were previously fitted to height-diameter data for tropical trees (Table 1).

Table 1. Shape of the height-diameter allometry. A total of ten different allometric models were fitted to relate total tree height (H in m) to tree diameter (D in cm) in the Ma'an and Mindourou sites in Cameroon. The Akaike Information Criterion (AIC), the Akaike weights (Aw), the Residual Standard Error (RSE) and parameter estimates are given for each model. The best model (lowest AIC and RSE, highest Aw) relating height to diameter is shown in bold for each forest type. Extracted from Fayolle *et al.* (2016)

Model	Ma'an site ($n = 251$, evergreen forest)						Mindourou site ($n = 270$, semi-deciduous forest)					
	AIC	Aw	RSE	a	b	c	AIC	Aw	RSE	a	b	c
Monotonic models												
(m1) Linear model, $H = a + b \times D$	1410.9	<0.001	3.99	18.39	0.168	–	1688	<0.001	5.47	19.38	0.195	–
(m2) Log-linear model, $H = a + b \times \log(D)$	1210.5	<0.001	2.68	−13.4	10.7	–	1583.8	0.126	4.51	−18.41	12.6	–
(m3) Power model, $H = a \times D^b$	1278.1	<0.001	3.06	6.7	0.363	–	1611.9	<0.001	4.75	6.51	0.392	–
Second-order polynomial models												
(m4) $H = a + b \times D + c \times D^2$	1279.7	<0.001	3.07	12.36	0.361	−0.00122	1612.4	<0.001	4.75	11.76	0.437	−0.00147
(m5) $H = a + b \times \log(D) + c \times (\log(D))^2$	**1187.4**	**0.330**	**2.55**	−39.74	24.86	−1.853	1584.4	0.093	4.51	−28.21	17.88	−0.676
(m6) $H = \exp(a + b \times \log(D) + c \times (\log(D))^2)$	1187.8	0.270	2.55	−0.473	1.566	−0.1492	1583.8	0.126	4.50	−0.085	1.365	−0.1184
Asymptotic models												
(m7) Monomolecular model, $H = a - b \times \exp(−c \times D)$	1189.6	0.110	2.56	37.5	35.9	0.0294	1585.9	0.044	4.52	44.7	40.4	0.0219
(m8) Gompertz model, $H = a \times \exp(−b \times \exp(−c \times D))$	1198.4	0.001	2.61	36.7	1.65	0.0397	1590.4	0.005	4.56	43.2	1.58	0.0316
(m9) Weibull model, $H = a \times (1 − \exp(−b \times D^c))$	1188.1	0.232	2.55	38	0.0398	0.919	1584.3	0.098	4.51	46.7	0.0437	0.826
(m10) Michaelis−Menten model, $H = a \times D/(b + D)$	1190.9	0.057	2.57	46.7	31.1	–	**1581**	**0.509**	**4.49**	55.2	38.2	–

We found that the Michaelis-Menten model provided good predictions (Fayolle *et al.* 2016) confirming the results obtained at plot level in French Guiana (Molto *et al.* 2014). It could appear

strange that I have ended first author of a study valorising data collected by a master's student who then became a PhD student, but the student was busy with his literature review (Loubota Panzou *et al.* 2016) and preparation of field missions. At the time, he was also lacking skills in modelling, but things have changed since. In this study, we found **between-site variation in height-diameter allometry** with lower trees in the evergreen forest than in the semi-deciduous forest for the same diameter (Figure 5), as already noticed by Longman & Jeník (1974) and by Henry *et al.* (2011). The latter, which reviewed biomass data and equations across the African continent, interpreted this result as a response to nutrient leaching in the wettest forests. In our study (Fayolle *et al.* 2016), we did include soil information collected in the frame of floristic analyses (Vleminckx *et al.* 2017) but we were not able to demonstrate between-site differences in soil fertility and to link soil and allometry variations. Interestingly, for the species shared by the two sites, we retrieved the same allometric pattern, trees tended to be shorter in the (wet) evergreen forest than in the (moist) semi-deciduous forest for a given diameter, suggesting an environmental control, though we fail to detect the environmental determinant.
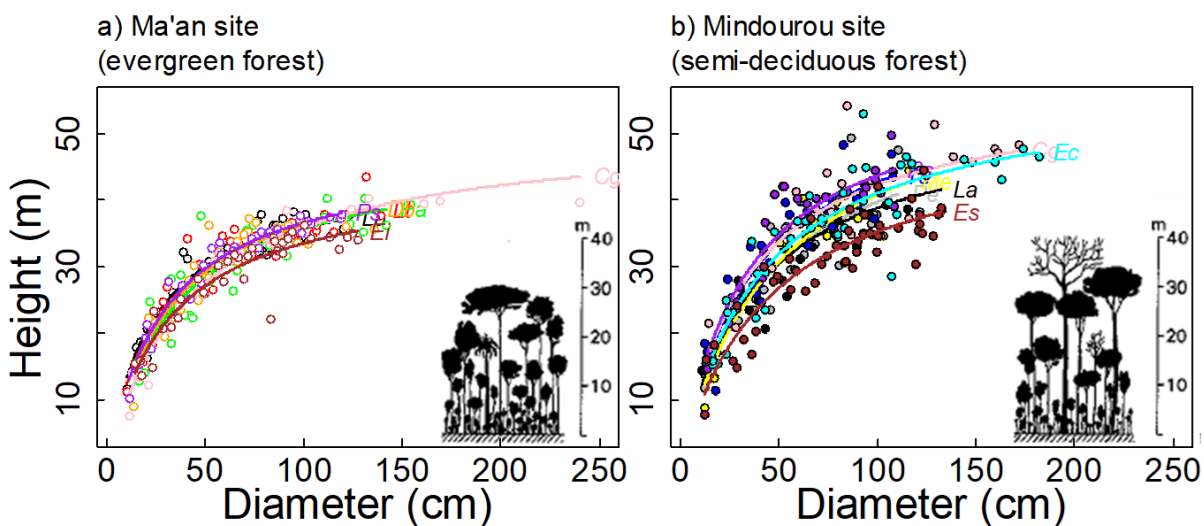

Figure 5. Height-diameter allometry of timber species in Cameroon. Trees were sampled in an evergreen forest, the Ma'an site (a) and in a semi-deciduous forest, the Mindourou site (b) and variation of canopy height among forest types with decreasing rainfall and increasing rainfall seasonality according to Longman & Jeník (1974) as inset. In (a) and (b), the curves correspond to the Michaelis-Menten model fitted for each species separately and colors correspond to species *Cylicodiscus gabunensis* (pink), *Distemonanthus benthamianus* (orange), *Entandrophragma cylindricum* (cyan), *Erythrophleum ivorense* and *E. suaveolens* (brown), *Lophira alata* (black), *Lovoa trichilioides* (red), *Milicia excelsa* (yellow), *Pericopsis elata* (grey), *Piptadeniastrum africanum* (green), *Pterocarpus soyauxii* (purple) and *Terminalia sperba* (blue). Adapted from Fayolle *et al.* (2016).

We extended the work on height-diameter allometry in the frame of the PhD of Grace Jopaul Loubota Panzou and we specifically developed a sampling design adapted to cover both the height-diameter allometry at the plot level and that of the dominant species. For the plot level

allometry, which is needed for accurate biomass estimates, we sampled all trees within one-hectare and all canopy trees intersecting a 20 × 20 grid over the 9-ha plots (300 × 300 m). The latter intended to capture large canopy trees for which tree height is most variable. These trees also have huge impact on the height-diameter models and on the biomass estimates at plot level. For the dominant species, we complemented the sampling so that to cover the entire diameter distribution of a set of species (> 30 species) selected based on their abundance, considering both stem density and basal area, to capture both small understory species strongly contributing to stem density and large canopy species strongly contributing to basal area (Loubota Panzou *et al.* 2018b). For all trees sampled, height was measured from two different points distant of approximately the tree height (Larjavaara & Muller-Landau 2013) and we also included additional measurements of crown dimensions, crown exposure to light (Sheil *et al.* 2006) and liana infestation (Rutishauser *et al.* 2011). This work was conducted in two sites in northern Congo, in permanent sample plots installed in the frame of the DynAfFor project by our colleagues from CIRAD. In the first site, we analysed the between-species variation in tree allometry, and developed **size-controlled allometric traits** (Loubota Panzou *et al.* 2018a). Among the 45 coexisting tree species in the moist and seasonal forest of the Loundougou site (1,600 mm yr^{-1} rainfall and a distinct dry season, DJFM), canopy species tended to be tall and with large crowns, light-demanding, wind-dispersed, deciduous, and large contributors to forest biomass (high basal area), while understorey species tended to be small-statured, shade-tolerant, animal-dispersed, evergreen and most abundant in terms of stem density, but we identified a **continuum of species** between these two extremes.

Between-species variation in allometry and allometric traits were further explored with the PreREDD+ dataset (Mankou *et al.* 2021). Species-specific allometric relationships were first fitted (Figure 6).
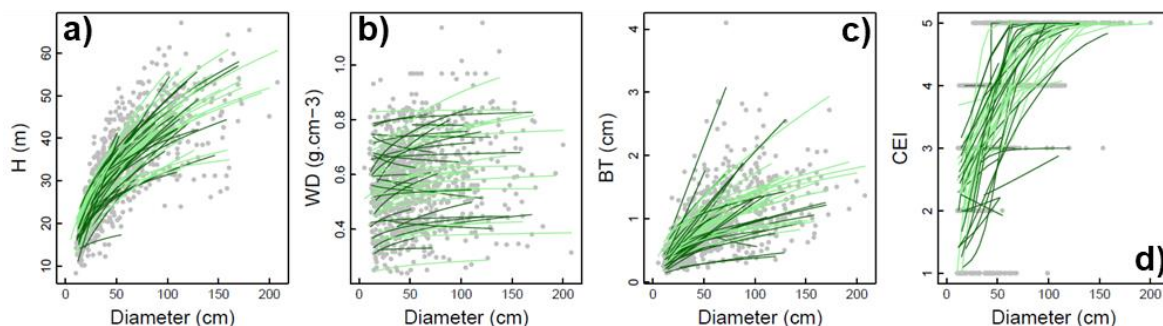

Figure 6. Species-specific allometries allowing to derive size-controlled traits. Species-specific allometric relationships between tree diameter and other tree measurements including total tree height (a), wood density (b) and bark thickness (c) were fitted using Ordinary Least Squares regressions after log-transformation and using ordinal regressions for the relationships between tree diameter and the crown

exposure index (d). One point represents one tree, and fitted lines represent species-specific relationships. The colors indicate the species leaf habit, deciduous (light green) *versus* evergreen (dark green) species. Extracted from Mankou *et al.* (2021).

These relationships were then used to derive allometric or size-controlled traits, such as height at 10 cm or height at maximum diameter, or crown exposure at 10 cm which is a good indicator of species light requirements (Poorter *et al.* 2003, 2006). We also computed the bark thickness at 10 cm, which is a key trait for fire tolerance that was only available for three forest species in Africa (Pellegrini *et al.* 2017) before our recent contribution with information for 50 species. Concerning wood density, we observed increasing, no, and decreasing trends with tree diameter, as observed from pith to bark for the same trees in an earlier study in the Malebo site, DRC (Bastin *et al.* 2015).

The same kind of sampling (abundant species), measurements (height, crown dimensions) and observations (crown exposure and lianas) were adopted in the frame of master's theses, in moist forest with the work of Arthur Chantrain in Luki, DRC, and with the work of Yorick van Hoef and Stevy Nna Ekomé in Bambidie, Gabon, and in miombo woodlands with the work of Pierre Jacques and Quentin Thibault in Mikembo, DRC. Therefore, we started to have a larger view of **crown allometry variations**. Available crown and stem data for tropical trees were specifically combined in the frame of the post-doctoral work of Grace Jopaul Loubota Panzou at the University of Exeter, UK, under the supervision of Ted Feldpausch (Figure 7).
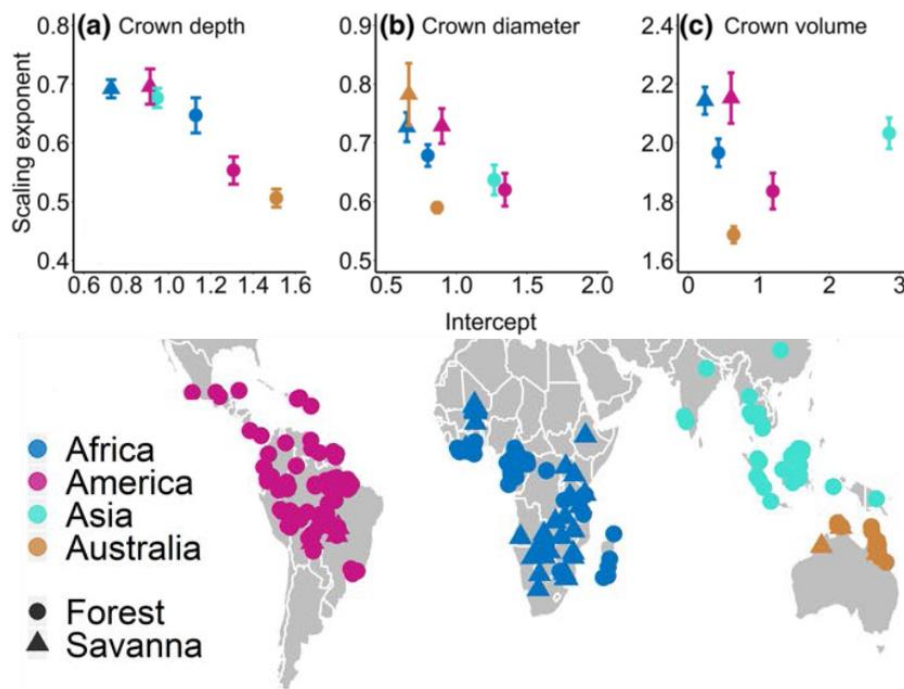

Figure 7. Pantropical variation in crown allometry. Allometric relationships (power law) relating tree diameter and (a) crown depth, (b) crown diameter and (c) crown volume, were fitted for each site, and

The final dataset contains 87,737 trees distributed among 245 forest and savanna sites across the tropics. Site-specific allometric relationships (power law) between crown characteristics (depth, diameter, and volume) and stem diameter were fitted and the values of the scaling coefficient and the intercept highlighted major differences in crown allometries between biomes (forest *versus* savanna) and also between continents for the same biome (Loubota Panzou *et al.* 2021) confirming an earlier cross-continent comparison in savannas (Moncrieff *et al.* 2014).

All these data collected in the frame of applied research were also used to test the predictions of the **Metabolic Scaling Theory** (MST, Figure 8) that makes several predictions about how different axes of tree size should scale against one another and notably predicts a scaling exponent of 2/3 for both tree height and crown radius with stem diameter and of 8/3 for biomass also with stem diameter (West *et al.* 1997, 1999). The MST have been developed applying principles of physics, chemistry and biology to explain the physiology and performance of individual organisms and thereby the structure of populations, communities and ecosystems (West *et al.* 1997, 1999; Brown *et al.* 2004). Predictions for the scaling of metabolic rates (photosynthetic rates) with body mass were first proposed by West (1997) based on the scaling of resource uptake and redistribution within optimized networks such as blood arteries and xylem vessels. Additional predictions were later provided for the scaling of height, biomass, diameter and leaf area in plants (West *et al.* 1999) and to plant growth and mortality (Brown *et al.* 2004) integrating stem biomechanics and relationships between metabolic rates and performance to the founding principles of plant water transport and branching architecture. The MST has been hotly debated, specifically its general nature and its underlying assumption of invariant scaling coefficients (*e.g.*, Zianis & Mencuccini 2004). For tropical forests, data from ten old-growth forests showed that there are no universal scaling relationships of growth or mortality with size among trees in tropical forests (Muller-Landau *et al.* 2006) and observed patterns were consistent with an alternative model considering changes in light availability with tree size. Our research activities provided tests of the MST predictions at two levels. At the biome level, our pantropical analysis of crown allometries (Loubota Panzou *et al.* 2021) showed values closed to the 2/3 exponent for savanna sites but lower values for forest sites (Figure 7), in agreement with earlier results of Shenkin *et al.* (2020). At the species level, we reported values of the scaling coefficient of tree height with tree diameter largely below the theoretical predictions of the MST (Figure 8a) for timber species in Cameroon (Fayolle *et al.* 2016). We also reported lower values for the scaling coefficient of tree AGB with tree height, with a mean of 2.45 (Mankou *et al.* 2021)

but only slightly different from the theoretical scaling exponent of 8/3, ~ 2.67, predicted by the MST (West *et al.* 1999).
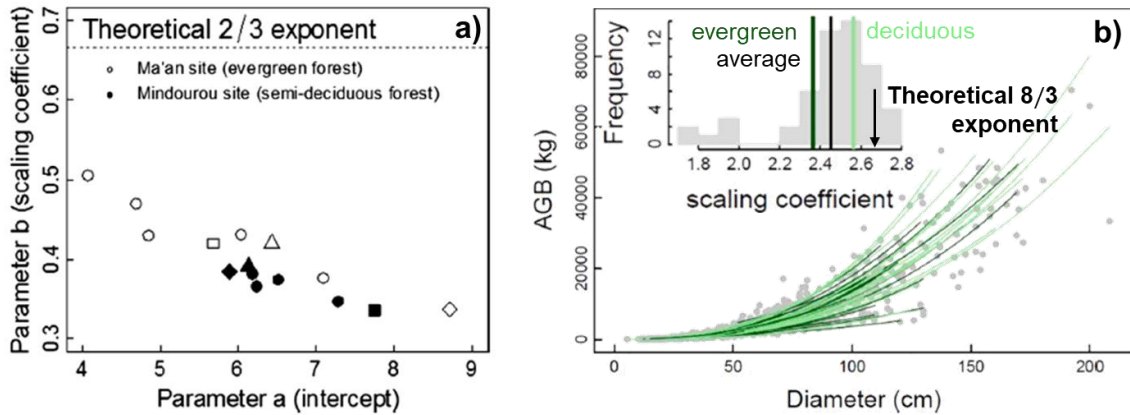

Figure 8. Prediction test of the Metabolic Scaling Theory. The theoretical value of the scaling exponent was confronted to estimated values for height-diameter allometry (a) of 12 timber species in Cameroon (Fayolle *et al.* 2016) and for AGB-diameter allometry (b) of 54 tree species sampled across central Africa (Mankou *et al.* 2021).

Beyond allometries and test of the predictions of the MST for different types of allometric relationships: height-diameter (Fayolle *et al.* 2016), crown-diameter (Loubota Panzou *et al.* 2021) and biomass-diameter (Mankou *et al.* 2021), we also worked on biomass allocation, and specifically mass allocation to crown. We indeed previously demonstrated (Ploton *et al.* 2016) that crown mass allocation increased with tree AGB, and we explored this pattern with the PreREDD+ dataset, complemented with the destructive data collected before (Fayolle *et al.* 2013a; Ngomanda *et al.* 2014) so that to have a large coverage across central Africa. Our results showed that the **allocation of biomass to crown increases with tree diameter** for most species (Figure 9), and that interspecific variation in the crown mass ratio (CMR, in %) was associated with the species dispersal mode and maximum height (Mankou *et al.* 2021). The CMR was highly variable among trees, from 1.2% and up to 84.2%, with a mean of 29.6%, and increased linearly with tree diameter. The coefficients of CMR models varied among the 54 tropical tree species, the relationships were mostly positive, though for some species, no and negative relationships were also retrieved. The intercept tended to be higher in average for evergreen species with a mean of 25% *versus* 14% for deciduous species, and this difference was significant. We also examined the relationships between the tree CMR and AGB for each individual species, and the pattern previously reported of a relatively constant CMR below 10 Mg, and of an increase in CMR with AGB above the 10 Mg threshold (Ploton *et al.* 2016), was also retrieved. The information on allometry, allocation, and traits we provided in this study (Mankou *et al.* 2021) could further be used in comparative ecology and for parameterizing

dynamic and succession models. We believe that Plant Functional Types (PFT) for tropical trees still needs to be investigated since grouping tropical tree species into meaningful groups of tree species is not straightforward (Swaine & Whitmore 1988) and only a few plant functional types are generally recognized in Dynamic Global Vegetation Models (DGVM, Fisher *et al.* 2018), generally two groups, evergreen *versus* deciduous tropical trees. In the successional model TROLL (Maréchaux & Chave 2017), up to 12 tropical plant functional types are recognized, and for each of them, the tree geometry is modelled explicitly with specific allometric relationships relating tree diameter, to height, crown radius and depth. Though plant functional types are at the core of many models of vegetation dynamics or of forest succession, the lack of information on allometry, allocation and traits, for some species and regions hampers models' predictions and this is particularly true for central Africa which is a largely under-sampled region.
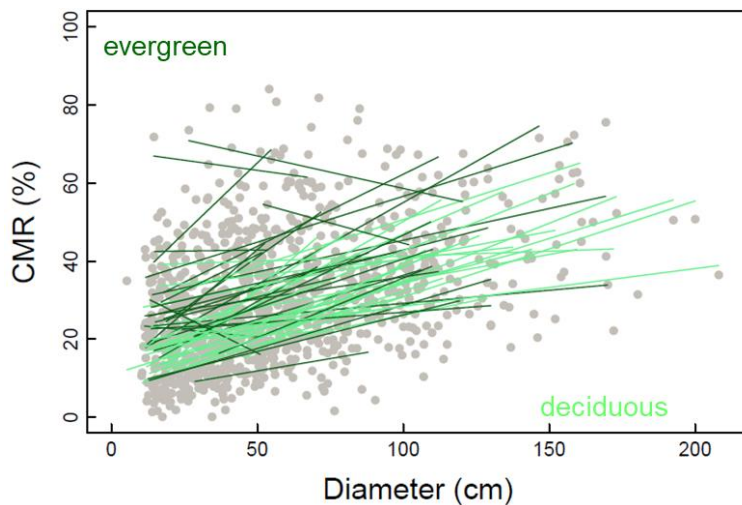

Figure 9. Interspecific variation in biomass allocation to crown. Species-specific linear relationships relating the tree Crown Mass Ratio (CMR, %) and diameter (cm) are shown for 54 tropical tree species destructively sampled across central Africa. One point represents one tree, and fitted lines represent species-specific relationships. The colors indicate the species leaf phenology, deciduous (light green) *versus* evergreen (dark green) species. Extracted from Mankou *et al.* (2021).

III.1.4. Forest biomass and carbon stocks

While the first step in the estimation of biomass and carbon stocks is the conversion of tree inventory data (diameter, species, and possibly height) into AGB estimates at the tree level, the second step corresponds to the sum of AGB estimates over all trees within the plots. The first plot-level biomass study I was involved in concerned two logging concessions in the Central African Republic (CAR) for which forest management inventory data were available and used to study the **spatial variation in biomass stocks** (Gourlet-Fleury *et al.* 2011). The results showed that basal area – the sum of cross-section of trees with a diameter at breast height greater than 10 cm – and AGB differ in their response to soil types, with physical constraints limiting basal area and biomass, but biomass being similar between resource-rich and resource-poor soils due to the environmental filtering of species with high wood density. This was later confirmed using the data from permanent sample plots installed on these two soil and forest types in the frame of

28

the DynAfFor project by our colleagues from CIRAD, the resource-rich soils on alluvium (Loundougou site, *Celtis* forest) and the resource-poor soils on Carnot sandstone (Mokabi site, *Manilkara* forest) on which slow growing and dense wooded species grows (Gourlet-Fleury *et al.* 2011; Fayolle *et al.* 2012) and the same AGB can be found due to compensation between tree volumes (related to basal area and height) and wood density (Loubota Panzou *et al.* 2018a).

During the last decade, and since our first review (Loubota Panzou *et al.* 2016), **inventory plots and biomass studies have flourished in tropical Africa**, including cross-site analyses for lowland terra-firme forests (Lewis *et al.* 2013) and more recently montane forests (Cuni-Sanchez *et al.* 2021), and across the global tropics (*e.g.*, Slik *et al.* 2013; Bastin *et al.* 2018; Hubau *et al.* 2020; ForestPlots.net *et al.* 2021). In central Africa several contributions can also be mentioned (*e.g.*, Bastin *et al.* 2014; Bauters *et al.* 2019; Djuikouo *et al.* 2010, 2014; Gonmadje *et al.* 2017; Kearsley *et al.* 2013). I was personally involved in the PhD of Grace Jopaul Loubota Panzou in northern Congo and he benefitted from the permanent sample plots installed by our colleagues from CIRAD in the frame of the DynAfFor project. I also supervised the master's thesis of several students. In 2018, Arthur Chantrain worked in Luki, DRC. In 2019, Jorick van Hoef and Stevy Nna Ekomé both worked in Bambidie, Gabon, and Pierre Jacques and Quentin Thibault worked in Mikembo, DRC, nearby Lubumbashi in the miombo woodlands and Olivier Bahati worked on the inventory data earlier collected in Bowa, also in the miombo woodlands of southern DRC. In 2021, Modestine Kompanyi worked on the massive forest inventory dataset earlier collected in the Lomami NP, the most recent park of the DRC, and which is located in a vastly undersampled and enigmatic area. In the later study, information on tree height was not available. To compare these sites, we computed a set of **forest attributes** (Table 2) following the terminology proposed by Poorter *et al.* (2015) and which includes stem density, basal area, Lorey's height – the average height of trees weighed by the basal area – for structural attributes, and mean wood density weighed by basal area which is generally considered as a compositional attribute. These attributes strongly vary within sites as shown for the two sites in northern Congo (Loubota Panzou *et al.* 2018a) because of the mosaic nature of tropical forest ecosystems, where gap dynamics might have opened the stand in one-hectare and not in the other hectares nearby. As a result, the basal area (Loubota Panzou *et al.* 2018a) and the density of large trees (Slik *et al.* 2010, 2013) remain strong determinants of AGB in intact forests, even if Lorey's height is also an important determinant notably when comparing continents and biomes (Saatchi *et al.* 2011). Indeed, across forest sites we found only little variation of Lorey's height and structural attributes in general, but miombo woodlands sites appeared structurally different from the forest sites (Table 2), with lower canopy (~ 15 m), basal area (≤ 20 m² ha^{-1}) and AGB (100-

150 t ha^{-1}). There is, however, structural variation related to climate and soils across intact closed-canopy tropical forests in Africa (Lewis *et al.* 2013), and across south-eastern woodlands and savanna (The SEOSAW Partnership 2021).

Table 2. Structural and compositional attributes of several forest sites and two miombo sites in central Africa. Sites are ordered from East to West, and North to South. For Lomami, the three values correspond to the average for the plots located on terra firme forest on clay soils, terra firme forest on sandy soils and seasonally flooded forest that were installed in the North and South part of the NP.

Site	Stem density (ha^{-1})	Basal area (m² ha^{-1})	Lorey's H (m)	Wood density (g cm^{-3})	AGB (t ha^{-1})
Forest					
Bambidie (Gabon, 32 ha).	385	28.8	30.6	0.64	367
Mokabi (Congo, 36 ha)	430	29.5	28.5	0.67	370
Loudoungou (Congo, 36 ha)	350	29.5	30.3	0.65	375
Luki (DRC, 8 ha)	442	28.2	27.6	0.66	326
Lomami (DRC, 18 ha)					
North (3 × 3 ha)	407;368;391	28.1;26.9;29.3		0.67;0.70;0.75	388;401;379
South (3 × 3 ha)	446;388;469	29.3;24.2;27.5		0.68;0.71;0.71	403;344;381
Savanna and woodland					
Bowa (DRC, 28 ha)	326	14.5	15.6	0.66	105
Mikembo (DRC, 10 ha)	484	21.1	15.1	0.69	154

Since the pioneering work of Brown (1989), there is now a general consensus on how to estimate AGB at the tree level (equation 1), using information on tree volume based on information on tree diameter (D in cm) and total tree height (H in m) combined (D²H) and information on wood density (ρ in g cm^{-3}) using species average (Molto *et al.* 2013; Chave *et al.* 2014). **An analogue reasoning to tree-level AGB has been proposed for plot-level AGB** (equation 2) that can be estimated from basal area (G in m² ha^{-1}), Lorey's height (H$_L$ in m) and wood density (ρ$_G$ in g cm^{-3}) weighed by basal area (Asner *et al.* 2012). The same kind of approach was also proposed using only the 20 top trees and successfully tested across the global tropics (Bastin *et al.* 2018).

$$AGB_t \sim \rho\, D^2\, H \tag{eq. 1}$$

$$AGB_p \sim \rho_G\, G\, H_L \tag{eq. 2}$$

While biomass itself might be less variable due to underlying offsetting (Gourlet-Fleury *et al.* 2011; Loubota Panzou *et al.* 2018a), integrating the response of biomass determinants, *i.e.*, the forest attributes individually, to environmental or disturbance factors, might help improve biomass estimates. For instance, in northern Congo, we did not detect any significant difference in mean AGB between the *Celtis* forest on alluvium and the *Manilkara* forest on sandstone, following our terminology (Fayolle *et al.* 2014a), while there were strong between-site differences in forest structure, composition and architecture (Loubota Panzou *et al.* 2018a). This **offsetting**

between forest attributes is the subject of the PhD thesis of Pauline Depoortere, funded by FNRS and supervised by Jean-François Bastin and me.

Concerning **biomass and carbon dynamics**, in their pioneer study, Lewis *et al.* (2009) first showed the extent of the carbon sequestration in intact tropical forests in Africa by comparing the amount of carbon stocks between two censuses. They showed that the net flux of carbon (the difference in carbon stocks) tended to be positive in most plots, and thus considered intact forests in Africa as a carbon sink. A long-term decline of this carbon sink has been observed in the Amazon (Brienen *et al.* 2015) and not yet in central Africa (Hubau *et al.* 2020) potentially because the data available did not include the last decade (2010-2020). Long-term monitoring of plots indeed remains difficult to maintain in central Africa, due to logistic and financial reasons. I had the chance to participate to the 2011 recensus of the site that has been monitored for the longest period in central Africa, the M'Baïki site in the CAR, where we were able to investigate the AGB dynamics thanks to the regular recensus of the permanent plots (40 ha in total), every two years at least, since installation in 1982 and silvicultural interventions in 1986 and 1987. We analyzed **recovery after logging** of both AGB and exploitable volume (Figure 10a and b).
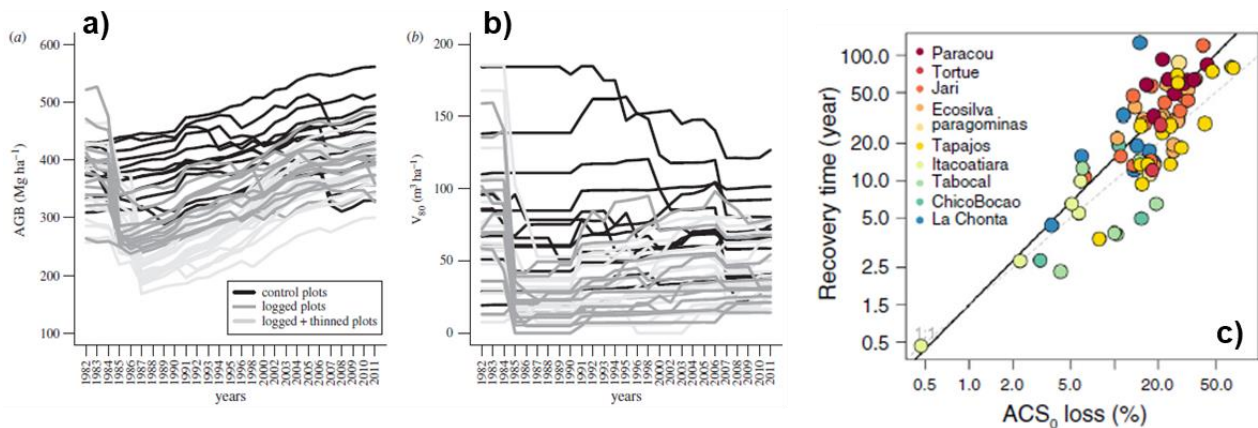

Figure 10. Tropical forest recovery after logging. Above-Ground Biomass (a, AGB) and volume recovery (b, V_{80}) after logging in the M'Baïki forest experiment, in the Central African Republic is extracted from Gourlet-Fleury *et al.* (2013) and relationship between time of recovery and percentage of initial above ground carbon stocks lost (ACS_0 loss) due to selective timber harvests and damage-induced mortality at 10 sites across the Amazon basin is extracted from Rutishauser *et al.* (2015).

In contrast to the timber volume, the forest biomass recovers relatively quicky after logging (Gourlet-Fleury *et al.* 2013) and the speed of recovery is proportional to the intensity of logging (Figure 10c) as shown across the Amazon basin by colleagues from CIRAD (Rutishauser *et al.* 2015). From an external point of view, the lack of recovery of timber volume could question the sustainability of logging, but in management plans, the first rotation cycle benefits from a primary forest premium, and it is admitted by forest administrations and managers that it is impossible to

recover the volume that has accumulated over centuries in natural forests, therefore volume recovery is 50% for the first cutting cycle and 100% recovery should only be achieved for the other cutting cycles.

With the M'Baïki data, we also analyzed the **contribution of large trees to biomass production** (Ligot *et al.* 2018b) following intriguing results published in Nature and interpreted as a continuous accumulation of carbon with tree size (Stephenson *et al.* 2014). The latter challenged the foresters' view who tried to adapt cutting cycles to forest productivity, which declines after a certain tree age and/or size in even-aged forests. In M'Baïki, large trees have high individual growth rates and also constitute a substantial amount of biomass as already demonstrated across the global tropics (Slik *et al.* 2013) but we showed with a dedicated bootstrap procedure that stand-level biomass production decreased with the abundance of large trees in all treatments (control, logged, and logged+thinned) and plots (of different sizes). Overall, the contribution of large trees to annual stand-level biomass production appeared limited in comparison to that of small trees. This pattern did not only originate from differences in abundance of small *versus* large trees or differences in initial biomass stocks among tree size classes, but also from a reduced relative growth rate of large trees and a relatively constant mortality rate among tree size classes. Large trees are increasingly gaining attention as being a valuable and a key structural characteristic of natural forests, but this study brought key insights to better gauge the relatively limited role of large trees in annual stand-level biomass production. In terms of carbon uptake, these results suggest, as already demonstrated in the Amazon basin (Rutishauser *et al.* 2015), a low net carbon uptake of old-growth forests in comparison to that of logged forests. Tropical forests that reach a successional stage with relatively high density of large trees progressively cease to be carbon sinks as large trees contribute sparsely or even negatively to the carbon uptake at the stand level, and negative net carbon fluxes generally correspond to large tree mortality (Rutishauser *et al.* 2010).

III.2. Forest types and biogeography of Africa

III.2.1. Forest types

In central Africa, forest legislations have been revised in the 2000s and management plans have become mandatory. The first step of forest management is to perform a **management inventory** that is used to determine the state of timber species populations, to quantify and map the timber resource, and to plan its exploitation over the 20-30 years of the rotation, in cutting

areas of equal volume each year. Therefore, vast amount of quantitative information on forest ecosystems have been collected by the forestry sector in central Africa, and more importantly, forest companies have used the comparable sampling design composed of consecutive 0.5-ha plots along transects covering the whole forest concession and distant of approximately 3 km apart (Figure 11). In the first inventory campaigns, all trees greater than 30 cm in diameter at breast height were measured in the plot (20 × 250 m) but species identification was restricted to trees belonging to a set of 79 species for which smaller trees, between 10 and 30 cm, were also inventoried in a subplot (in red, Figure 11), while during the subsequent inventories all trees greater than 20 cm in diameter were identified to species (in black).
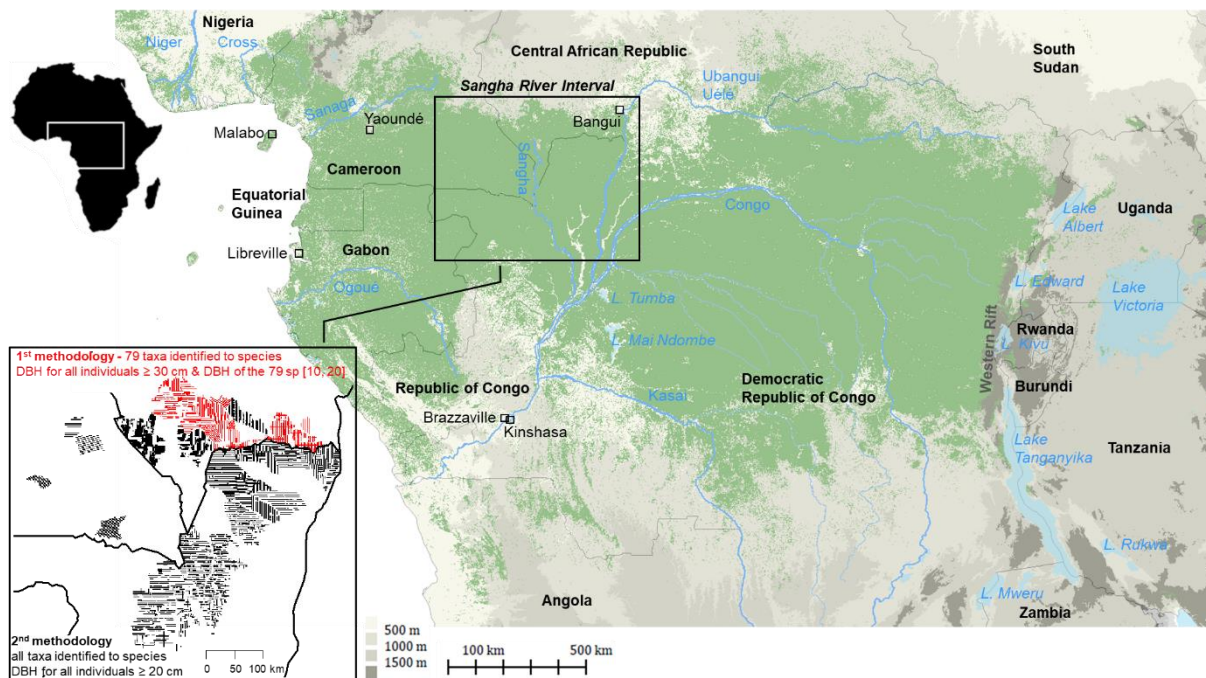

Figure 11. Forest inventory data in the Sangha River Interval. The location of the Sangha River in central Africa is shown on a background map of forest cover (in green) and altitude (in grey) respectively adapted from GLOBCOVER and SRTM. The forest management inventories available and analyzed in the frame of the CoForChange project are shown as inset.

The inventory data used for management planning of logging concession were first combined for the Central African Republic (CAR), thanks to the PARPAF project funded by the French Agency for Development (AFD) and analyzed in the frame of the PhD thesis of Maxime Réjou-Méchain. These data were first used to identify variation in tree species composition across the forested part of the country (south-west) and underlying determinants (Réjou-Méchain *et al.* 2008) and the **unique species composition of forest growing on Carnot sandstone** was highlighted confirming earlier observations (Lanly 1966; Boulvert 1986) and knowledge of forest managers. Together, we also later demonstrated that the quantitative information these commercial

inventories contained is reliable (Réjou-Mechain *et al.* 2011). We specifically compared the alpha and beta diversity retrieved in the plots sampled by the field workers and in the same plots sampled by experienced botanists in four logging concessions, and that separately for small and large trees (Table 3).

Table 3. Validity of commercial inventories. Consistencies of alpha and beta diversity patterns between the commercial and the control inventories were tested with Spearman's or Pearson's (for Mantel analyses) correlation coefficients. All values were found highly significant ($P \leq 0.001$) following the Spearman's rank correlation tests or the Mantel's permutations tests (n=999). For ordination analyses, the explained variance of the two first axes ranged from 3.5% to 11% for the correspondence analyses (CA) and from 7.1% to 32.4% for the non-symetric correspondence analyses (NSCA). Extracted from Réjou-Méchain *et al.* (2011).

Concession	Alpha diversity		Beta diversity					
	Species richness	Inverse Simpson	Ordinations				Mantel	
			CA		NSCA		Jaccard	Morisita–Horn
			Axis 1	Axis 2	Axis 1	Axis 2		
Small (<10 cm DBH)								
1	0.65	0.69	0.80	0.83	0.81	0.82	0.65	0.69
2	0.65	0.63	0.35	0.46	0.66	0.70	0.51	0.52
3	0.83	0.75	0.21	0.66	0.80	0.76	0.71	0.75
4	0.78	0.74	0.67	0.81	0.77	0.89	0.75	0.76
Large (<30 cm DBH)								
1	0.81	0.86	0.92	0.96	0.96	0.93	0.86	0.89
2	0.68	0.65	0.80	0.41	0.83	0.68	0.61	0.65
3	0.85	0.80	0.97	0.85	0.96	0.60	0.85	0.87
4	0.80	0.82	0.72	0.90	0.94	0.84	0.83	0.85

I later participated in the collation of forest inventory data at a larger scale (> 100,000 plots of 0.5 ha) across the **Sangha River Interval** in the frame of the CoForChange project during which I was a post-doctoral fellow (Figure 11). In this project, we extended the work done in the CAR to the neighboring countries, namely eastern Cameroon, and northern Congo, around the Sangha River, a big affluent of the Congo River. I first worked at the species level, on a restricted set of species well identified in all logging concessions and I found a strong impact of the geological substrate on **tree species distributions** focusing on 31 timber species. I identified species able to grow on the sandy soils that develop on the Carnot sandstone, and species never found on this geological substrate (Fayolle *et al.* 2012), notably species with high nutrient demand such as *Triplochiton scleroxylon* (ex-Sterculiaceae, now Malvaceae), *Ceiba pentandra* (ex-Bombacacea, now Malvaceae), and *Terminalia superba* (Combretaceae) that are recognized indicators of soil fertility locally, notably for cocoa production (Guillot 1981).

Then, I worked at the plot level to identify large-scale variations in the structure, composition and functioning of African moist forests (Fayolle *et al.* 2014a). I identified seven forest types and most of the study area was composed of a mosaic of the structural derivatives of the *Celtis* (ex-Ulmaceae, now Cannabaceae) forest confirming earlier description of forests dominated by Ulmaceae and Meliaceae (Boulvert 1986). Among the other forest types, secondary *Musanga*

34

(Moraceae) forest was found in repeatedly disturbed areas, along roads and around main cities while mixed *Manilkara* (Sapotaceae) forest covers a huge area on the Carnot sandstone earlier mentioned, in the southern CAR and in northern Congo, and monodominant *Gilbertiodendron* (Fabaceae) forest was found to be sparsely distributed along rivers. The latter forest type is an intriguing system (with up to more than 50% of the stems belonging to the same species, *Gilbertiodendron dewevrei*) that can be found throughout the Congo basin and that has deserved a lot of attention (*e.g.*, Hart *et al.* 1989; Torti *et al.* 2001; Peh *et al.* 2011a, b) including paleoecological approaches (Tovar *et al.* 2019).

Among traits, and beyond wood density earlier explored (Gourlet-Fleury *et al.* 2011), we further focused on **forest decidousness** (Condit *et al.* 2000) which was found to differ among forest types (Fayolle *et al.* 2014a) and to respond differently to climate across geological substrates (Ouédraogo *et al.* 2016). We indeed found that the percentage of deciduous trees increased with the severity of the dry season (Figure 12) estimated with the Maximum Climatological Water Deficit (MCWD) earlier proposed for the Amazon basin (Malhi *et al.* 2009). This increase strongly varied with the geological substrate, geology being three times more important than the rainfall regime in explaining the total variation in deciduousness. Tropical forest deciduousness is the result of both the advantage of deciduous species in climates with high rainfall seasonality, and the persistence of evergreen species on resource-poor soils confirming our earlier work on the **importance of habitat filtering on sandstone substrate** (Gourlet-Fleury *et al.* 2011; Fayolle *et al.* 2012, 2014a; Réjou-Méchain *et al.* 2014).
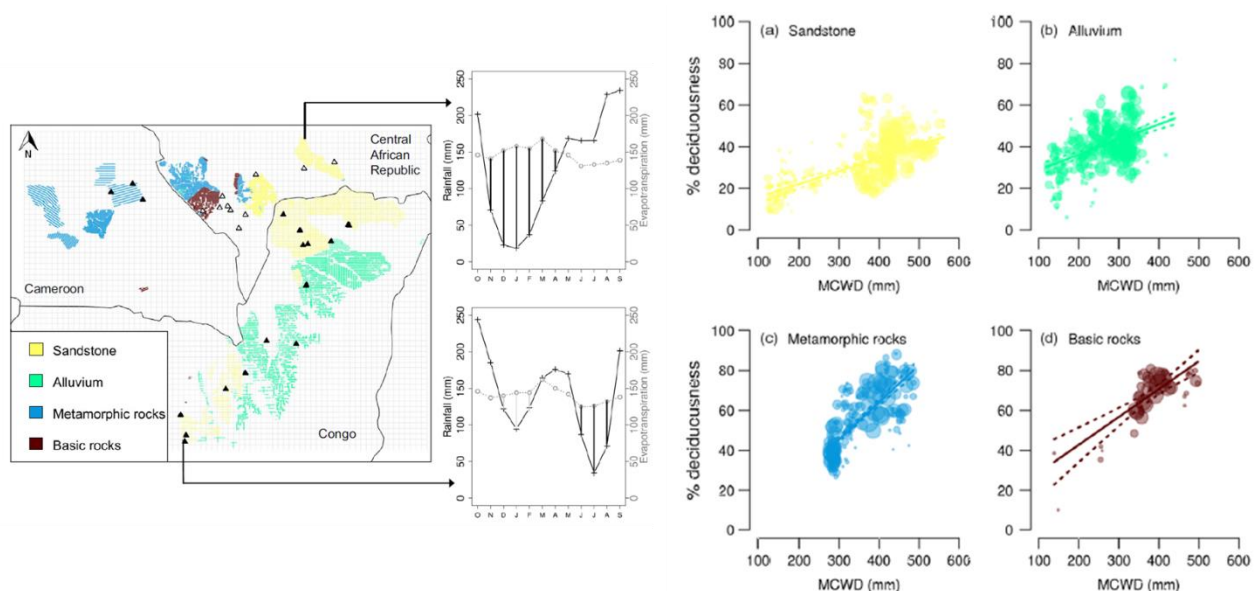

Figure 12. Forest deciduousness in the Sangha River Interval. The location of the 62,624 0.5-ha plots colored according to the geological substrate is shown, so as that of the 19 soil pits dug for the purpose of

this study (filled triangles), and of the 18 pits gathered from published studies (empty triangles). The 8 × 8 km grid (light grey) used to compute the fraction of deciduous trees and country borders (dark grey) are shown in background. The right panel shows two contrasting grid cells in terms of rainfall regime (black crosses) and evapotranspiration (grey circles). The main seasonal cycle of rainfall is a pronounced dry season during boreal winter. In the south of the area, this pattern is associated with an additional short dry season during boreal summer. During dry seasons, evapotranspiration is higher than rainfall, the difference between evapotranspiration and rainfall being the water deficit (WD, in mm). For each dry season, a cumulative WD over the dry months can be computed as the sum of WD over those dry months (area hatched). Maximum climatological water deficit (MCWD) is defined as the cumulated WD of the driest dry season, *i.e.*, the dry season with the greatest cumulated WD (area hatched in black). Relationships between forest deciduousness (%) and MCWD for the four geological substrates – (a) sandstone, (b) alluvium, (c) metamorphic rocks and (d) basic rocks) – with model fitted values (solid lines) and 95% confidence intervals (dotted lines). Symbol size corresponds to sampled area that was used as weights in the model. Extracted from Ouédraogo *et al.* (2016).

Finally, this kind of approach, combining commercial inventories, trait information, and environmental determinants, was extended at the scale of central Africa (Réjou-Méchain *et al.* 2021), using additional forest inventory data in Cameroon, in Gabon and in the DRC. Forest types were identified and mapped at a larger scale thanks to a **predictive ordination approach** developed by our colleagues at CIRAD and implemented into an R package (Mortier *et al.* 2016). This work was published in Nature and the map of forest types earlier presented in this manuscript (Figure 1b) is the first comprehensive map of forest types across central Africa and will be very useful for forest management and conservation in the region.

III.2.2. Forest history

According to White (1979, 1983), the whole of the moist forest biome in Africa is included in the vast Guineo-Congolian Region which is further divided into three subcentres of endemism, from West to Est, the Upper Guinea, the Lower Guinea and the Congolia, being interspersed by the Dahomey Gap, and by the Sangha River Interval. The studies earlier described and related to the CoForChange project were conducted in the Sangha River Interval, a vast forest area, 400 km wide (14 - 18°E) located between Lower Guinea and Congolia, recognized for its low endemism, and **suspected to have been a savanna corridor** between 3,000 and 2,500 years BP (Maley 2002). This event, later called the '***third millennium BP crisis*** *of the central African rainforest*' (Ngomanda *et al.* 2009) was well recorded in sediments collected in several swamps and lakes from Atlantic central Africa (Vincens *et al.* 1999) but most of the soil profiles studied in the CoForChange project, which covers the entire Sangha River Interval, did not show a massive savanna development between 3,000 and 2,500 years BP (Bremond *et al.* 2017). Important disturbances, such as short but intense rainfall changes, might have damaged the mature forest and allowed brief development of pioneer species or secondary forests, but

savanna only developed on the edges of the forest block. Biomass burning remained relatively constant until 1,500 yr cal. BP (Tovar *et al.* 2014) which means that the impact of Bantu populations' migrations was probably limited and that the vegetation changes recorded at the edge of the forest block are indeed due to climate rather than human activities though it has been hotly debated (*e.g.*, Bayon *et al.* 2012a; Maley *et al.* 2012; Bayon *et al.* 2012b).

In the frame of the PhD thesis of Julie Morin-Rivat who was supervised by Jean-Louis Doucet and Hans Beeckman, we collaborated on forest paleoecology and history in central Africa. **Human populations have long inhabited the moist forests of central Africa** as demonstrated by the vast amount of evidence of human presence and activities (Figure 13) we have retrieved throughout the Sangha River Interval (Morin-Rivat *et al.* 2014). Frequent and abundant charcoals, and also potsherds and oil-palm endocarps were also observed in the Campo Ma'an area in Cameroon (Biwolé *et al.* 2015) in the frame of the PhD thesis of Achille Biwole, who was also supervised by Jean-Louis Doucet.
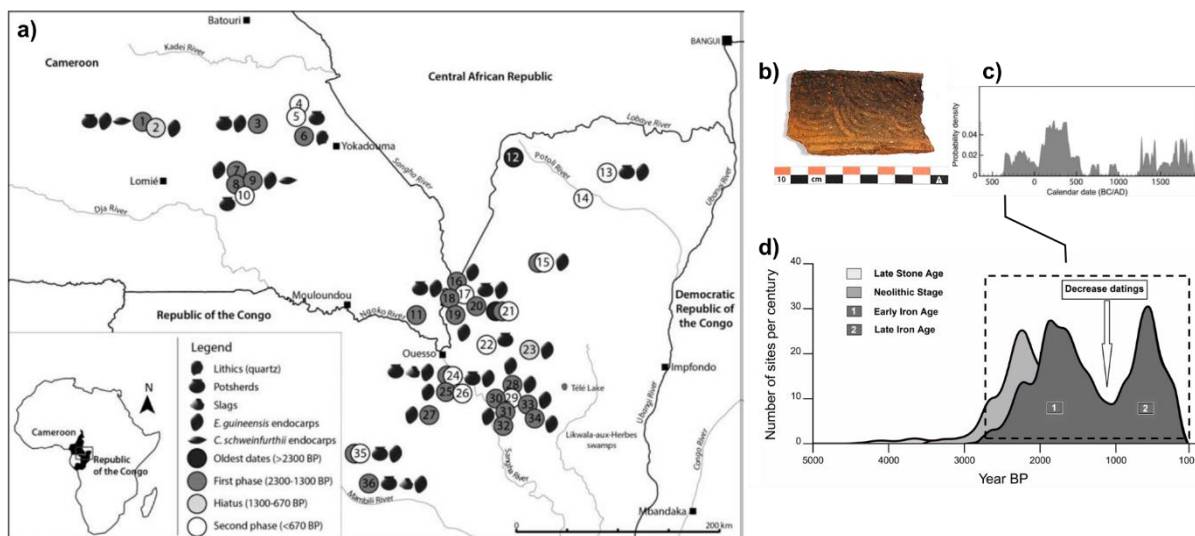

Figure 13. Evidence of human presence during the late Holocene in the Sangha River Interval. Location of the sites (a) according to the four phases as well as the type of archaeological and archaeobotanical findings such as potsherds (b). The summed probability distribution of the dates (c) calibrated in BC/AD, n = 41 dates (two oldest dates were excluded: KIA-38067 and Poz-41789). Note that dates are concentrated in two time periods, centered on 2300–1300 BP (350 BC–AD 650) and after 670 BP (after AD 1280). Extracted from Morin-Rivat *et al.* (2014). The temporal distribution of the radiocarbon dates over the 5000-100 cal BP period and the corresponding cultural traditions from the larger study of Oslisly *et al.* (2013) is also provided (d).

Our analyses of 43 radiocarbon dates from the Sangha River Interval (Morin-Rivat *et al.* 2014) extending from 15,000 BP to the present time showed a bimodal distribution in the Late Holocene, which was interpreted as two phases of human expansion in central Africa with an intermediate phase of depopulation. The 2,300–1,300 BP phase is correlated with the migrations

of supposed farming Bantu populations from northwestern Cameroon. Between 1,300 and 670 BP, less material could be dated. This is in agreement with the decrease dating generally reported for central Africa (Figure 13d) and interpreted as a massive collapse of human population of unknown origin yet (Wotzka 2006; Oslisly *et al.* 2013). Following this, the 670–20 BP phase corresponds to a new period of human expansion known as the Late Iron Age.

More recently, the **abandonment of human settlements and activities in the forest during the colonial era have fingerprinted present-day forests** in terms of structure and composition (Morin-Rivat *et al.* 2017). The canopy of tropical forests in central Africa is indeed dominated by large-statured light-demanding species (Loubota Panzou *et al.* 2018b) and the abundance of these light-demanding species in the canopy is most probably related to historical disturbances caused by human land use between three to four centuries ago as earlier suggested in Nigeria (Van Gemerden *et al.* 2003). These light-demanding species dominating the canopy generally show a diameter distribution deviating from the classical reverse-J (with many small trees) but instead show a flat or unimodal distribution lacking small trees. This is the case for many timber species and this regeneration failure has often been mentioned in forest management plans. Also in the frame of the PhD of Julie Morin-Rivat, we used commercial forest inventory data earlier mentioned for identifying species with unimodal distribution of diameters and we estimated the age of the trees corresponding to the mode of the diameter distribution using growth data and models (Figure 14). After the fit of several growth models relating tree diameter to mean annual diameter increment, ordinary differential equations were solved numerically to establish relationships between tree diameter and time (age) and the age of trees at the mode was then converted into dates (insets on Figure 14). This allowed us to demonstrate that the regeneration shortage began around 1850 after major anthropogenic disturbances ceased in the forest probably because the colonial administrations concentrated people and villages along primary communication axes. People formerly gardened the forest by creating scattered openings, which were sufficiently large for the establishment of light-demanding trees and the regeneration shortage observed today for these species is attributed to the less itinerancy and disturbance in the forest. It was also demonstrated in Gabon that demographic drivers alone cannot explain such unimodal distribution of diameters (Engone Obiang *et al.* 2014) and the authors concluded that their "*results reinforce the view of a forest that is constantly changing and shaped by past human perturbations*".
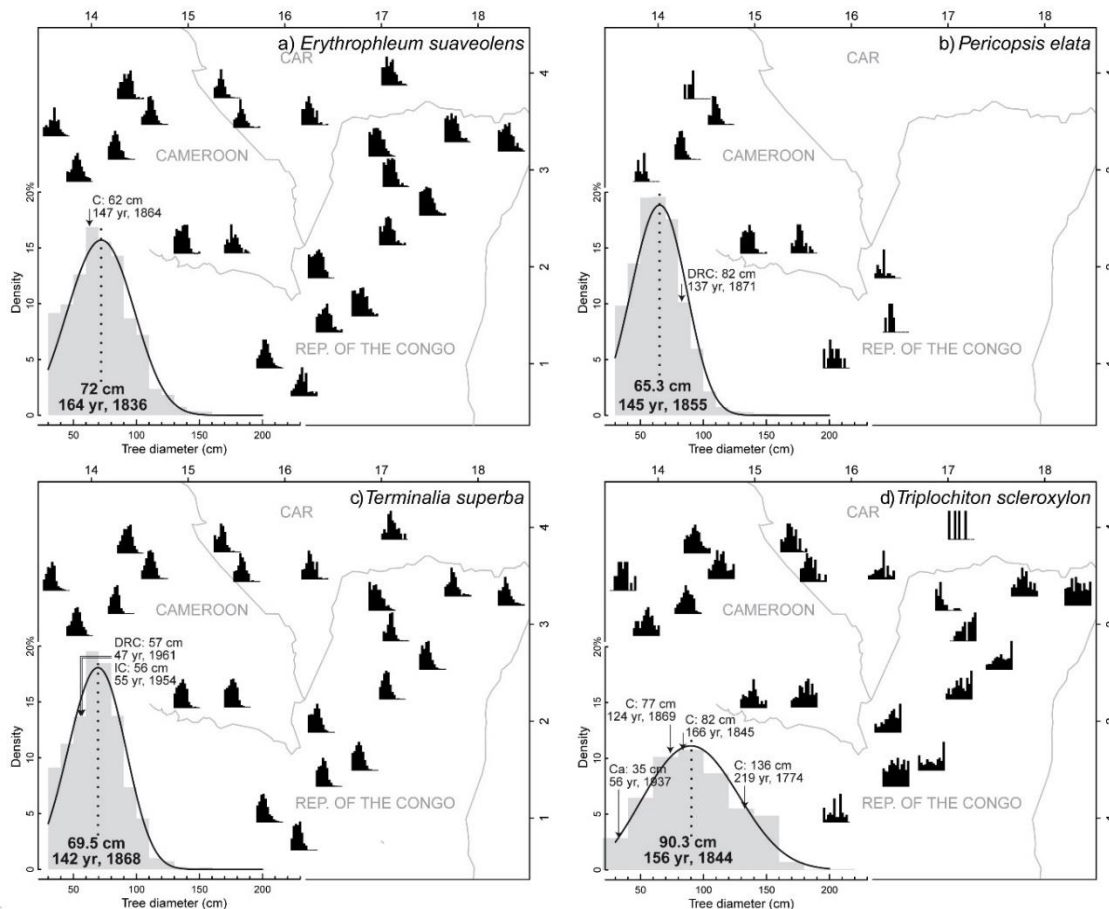
Figure 14. Diameter distribution of ageing, declining tree populations. The distribution of diameters of four canopy tree species is shown for 22 logging concessions (black). The solid lines on the average diameter distributions (gray) correspond to the fitted parametric diameter distribution (Weibull), which was used to estimate the mode and corresponding age. Ages and dates (AD) in the Sangha River Interval were estimated using the mean annual increment of diameter of a) 367 *Erythrophleum suaveolens*, b) 199 *Pericopsis elata*, c) 152 *Terminalia superba* and d) 265 *Triplochiton scleroxylon*. Age estimations were validated with published tree-ring data for these four species in natural forests in Cameroon (C), the Democratic Republic of Congo (DRC) and the Ivory Coast (IC) that are shown in the Supplementary Information of Morin-Rivat *et al.* (2017).

III.2.3. Biogeography of Africa

A huge amount of work was done to identify and map the forest types in central Africa, and at a larger scale, studies of the biogeography of the African continent mostly revisited the phytochoria and transition zones between them identified by White (1979, 1983), see for instance the work of Linder *et al.* (2005, 2012) and of Droissart *et al.* (2018). Given the fact that commercial forest inventory data are always suspected of incomplete and even unreliable taxonomic information, with my colleague Mike Swaine from the University of Aberdeen, UK, we started assembling tree species lists for forest sites across the Guineo-Congolian Region (west

and central Africa). This idea raised because we wanted to complement the work on the forest types made with commercial inventory. Also, the growth data of timber species in M'Baïki were used throughout the Congo basin for forest management planning, and we wondered whether it was a safe practise, because M'Baïki is located at the northern margin of the Congo basin forests. Given his past research activities in Ghana, Mike Swaine provided huge amount of data for the country, he carefully screened the literature in English, and I was charged to check the literature in French, dating back from the colonial era and including vast amounts of grey and dusty literature. Our first analysis was restricted to the Guineo-Congolian Region (including west and central Africa), but I met Andy Plumptre in a phenology workshop in Uganda in 2012, and he opened the door to many tree species lists across east Africa, so that we ended into 455 sample sites scattered across tropical Africa (Figure 15a), including several types of tropical forests (wet, moist, dry, and lowland to moderate elevation montane forests) but excluding montane (> 1,000 m asl) and swamp forests.
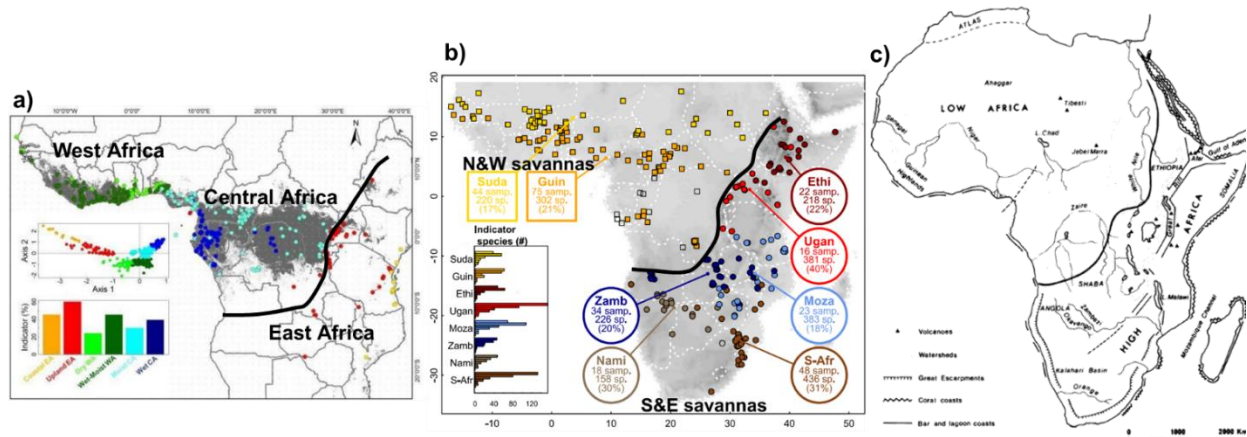

Figure 15. Sharp floristic discontinuity (thick black line) across sub-Saharan Africa identified with (a) forest tree species composition (Fayolle *et al.* 2014b), (b) savanna tree and shrub species composition (Fayolle *et al.* 2019) and (c) based on the physical environment (White 1983).

I used classical tools in vegetation analyses, namely ordinations (correspondence analysis) followed by Ward's clustering, to identify large-scale variation in tree species composition across tropical African forests and identify the environmental determinants (elevation and 19 climatic variables extracted from the BIOCLIM data). Beyond the three floristic regions and clusters identified within these regions: Coastal and Upland for East Africa, Dry and Wet-Moist for West Africa, and Moist and Wet for Central Africa (Figure 15a), and their indicator species (Dufrêne & Legendre 1997), the most important result obtained to my point of view is the **major floristic discontinuity located at the Albertine rift** that separated the dry, moist and wet forests of West and Central Africa (the entire Guineo-Congolian Region) from the upland and coastal forests of East Africa. Except for the Albertine Rift, no evidence was found to support the other

40

proposed floristic discontinuities such as the Dahomey Gap which has been considered for long as the division between Upper and Lower Guinea (White 1979, 1983). Two main environmental gradients were detected. The rainfall gradient was strongly correlated with the variation in tree species composition in West and Central Africa. The elevation/temperature gradient highlighted the major floristic differences within East Africa and between East Africa and the Guineo-Congolian Region, the latter being most probably due to the geological disruption and associated climatic history of the East African uplift (Sepulchre *et al.* 2006).

A few years later, Mike Swaine proposed me a follow up study on the **woody species composition of savannas and woodlands across (sub)tropical Africa**, he already had started assembling tree and shrub species lists published in English, and again I oversaw compiling information published in French. I also lead the data analyses and I used the same kind of approach developed for the forest study (Fayolle *et al.* 2014b) and which fits the roadmap of Kreft & Jetzt (2010) earlier proposed for identifying bioregions. The preliminary results were presented in 2017 in Brussels at the GTOE conference during a symposium on African woodlands co-organized by Casey Ryan from the University of Edinburgh, UK and by Manfred Finckh from the University of Hamburg, Germany, who both further contributed to new species lists from eastern and southern woodlands, respectively. In the end, I analyzed the composition of woody species lists for 298 samples of savanna vegetation across Africa, extending from 18°N to 33°S and from 17°W to 48°E (Figure 15b). Using Ward's clustering directly on the samples dissimilarity matrix, that was computed with the Simpson index of beta diversity which is known to be richness independent (Koleff *et al.* 2003), I identified eight floristic clusters across African savannas which in turn were grouped into two larger macro-units. Ordinations at species and genus levels showed a clear differentiation in woody species composition between the North & West macro-unit and the South & East macro-unit. This **floristic discontinuity** was already identified in the forest study (Fayolle *et al.* 2014b) and matches to the Low (*i.e.*, North & West) and High (South & East) division of Africa previously proposed by White (1983) and which tracks climatic and topographical variation. In the North & West savannas, the floristic gradient determined by rainfall was partitioned into the Sudanian (drier) and Guinean (wetter) clusters. Within **the highly heterogeneous savannas and woodlands of South & East Africa**, six clusters were identified: Ugandan, Ethiopian, Mozambican, Zambezian, Namibian and South African. This heterogeneity in floristic composition was further explored in the SEOSAW project (The SEOSAW Partnership 2021) but including other life forms might have helped refining savanna types, as suggested by the results of Droissart *et al.* (2018) using species occurrence derived from herbarium records.

In the frame of the PhD thesis of Davy Fonteyn, we have been developing a similar approach but for **terrestrial mammals in central Africa**. Tropical forests in central Africa have long been recognized for the diverse and iconic mammalian fauna they shelter, but how assemblages are spatially structured is still barely known, though being crucial for coordinating regional conservation actions. Similarly to my earlier forest and savanna studies (Fayolle *et al.* 2014b, 2019), we have made an extensive compilation of species lists derived but for forest-dwelling mammals, encompassing both wildlife and bushmeat-related surveys. We focused our analyses on carnivores, primates, and artiodactyls because these three orders hold the best sampling coverage in the combined dataset (31, 64, and 49 species retrieved respectively, and 307, 514 and 386 sites) and their identification at the species level is better resolved and less prone to identification errors (contrary to rodents, which pose important identification challenges). On the combined dataset, we applied a beta-diversity approach (dissimilarity in species composition) to delimit zoogeographic districts. We specifically computed the Simpson index of beta-diversity for all pairs and clustered surveys with similar composition using Ward's algorithm. While carnivores only form a unique and broad Congolian district with no clear further divisions, both primates and artiodactyls present spatially structured assemblages (Figure 16), and the distribution of the eight primate and six artiodactyl districts revealed a **highly congruent zoogeographic regionalization across central Africa**. The number of clusters we retained depended on three criteria: the average silhouette values, the number of significant indicator species (Dufrêne & Legendre 1997), and the spatial pattern (clustered distribution). In addition to the zoogeographic regionalization, we identified the environmental determinants of the districts' distribution with a random forest approach that confirmed the prominent role of rivers in structuring primate and artiodactyl assemblages, as earlier shown for guenons in the Congo basin (Colyn *et al.* 1991). Here, the Ubangui/Congo River systems was associated to the first split in primate and artiodactyl assemblages, and then the Cross and Sanaga Rivers further divided assemblages in Atlantic central Africa. Rainfall was also found an important determinant of primate districts' distribution, and specifically for distinguishing the Atlantic and Inland districts, whose boundary coincide with the transition between evergreen and semi-deciduous forests in Atlantic central Africa driven by rainfall (Réjou-Méchain *et al.* 2021). The contrasted primate assemblages between evergreen and semi-deciduous forests is most likely the results of differential quality, quantity and seasonality of fruits, seeds and leaves, the main components of a primate's diet. Lastly, we used our random forest classification model to map the zoogeographic districts across central African forests, highlighting priority districts that are threatened and poorly represented in the protected area network. Concerning conservation management, the district species pool can be employed to assess species loss in newly sampled areas and to target species for rewilding

opportunities. While ongoing and future climatic changes and human population growth jeopardize forest-dwelling mammal species and their assemblages, our study also highlights those vast areas of the Congo basin that remain undersampled, calling for more field data collection in priority areas.
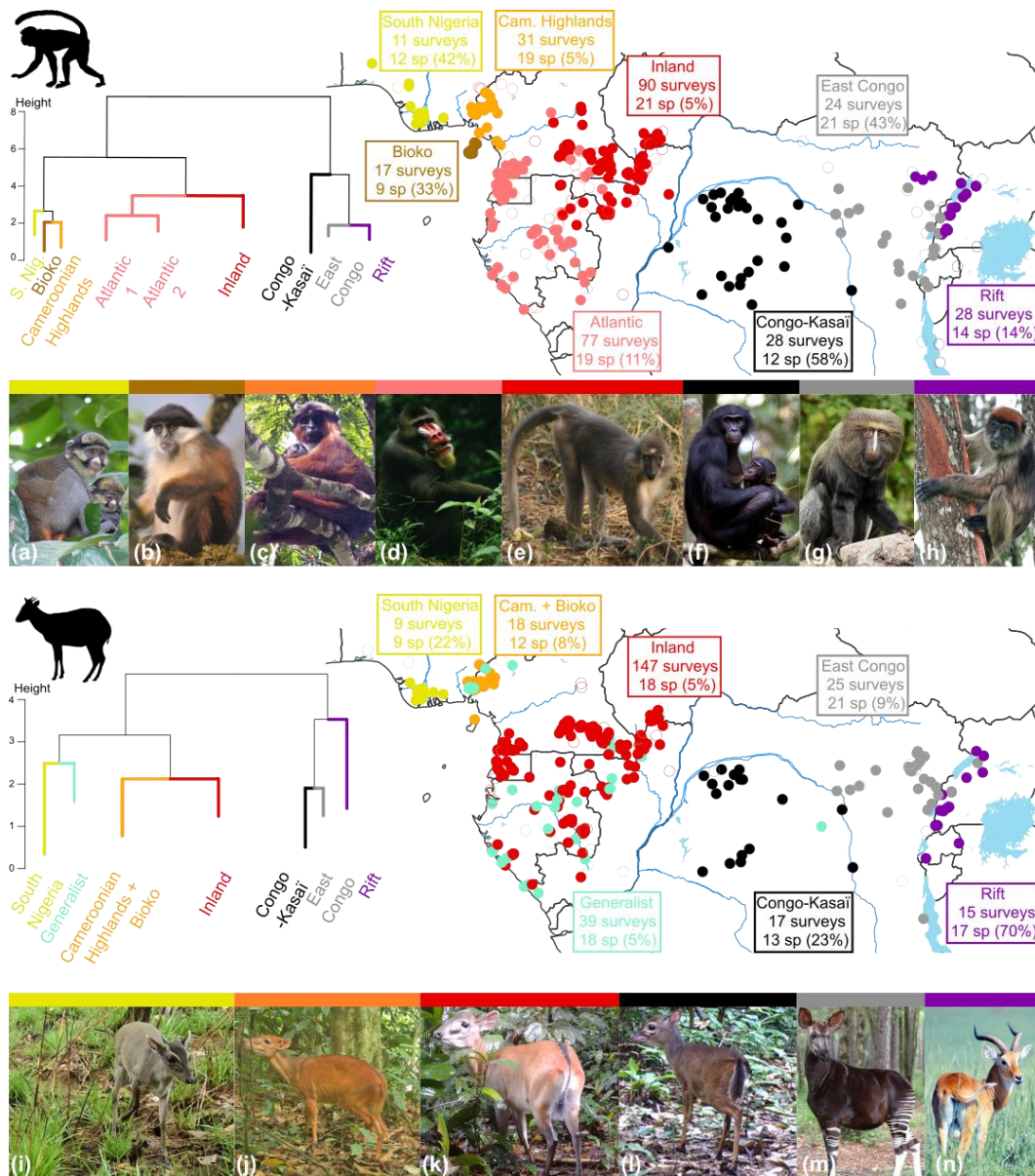
Figure 16. Congruent regionalizations between primates and artiodactyls across central Africa. The dendrograms (Ward's algorithm on Simpson dissimilarity) show the relatedness between districts that are also displayed on the map. Filled and empty circles respectively correspond to silhouette scores greater and lower than 0.2. The species pool, the proportion of indicator species and the number of surveys (with a silhouette score > 0.2) is given for each district. Animal photographs display important indicator species of each district following the same color scheme. Species name and photo courtesy are given for primates, *Cercopithecus sclateri* (a) by Lynne R. Baker, *Piliocolobus pennantii* (b) by Richard A. Bergl, *Piliocolobus preussi* (c) by A.N. Hofner, *Mandrillus sphinx* (d) & *Cercocebus agilis* (e) by Brent Huffman/UltimateUngulate, *Pan paniscus* (f) by Takeshi Furuichi, *Cercopithecus hamlyni* (g) by Paul

43

Moine, *Piliocolobus tephrosceles* (h) by Thomas T. Struhsaker; and for artiodactyls, *Philantomba walteri* (i) by Délagnon Assou, *Cephalophus ogilbyi* (j) by WCS Nigeria, *Cephalophus leucogaster* (k) by Davy Fonteyn, *Philantomba simpsoni* (l) by John Hart/Frankfurt Zoological Society TL2 Project, *Okapia johnstoni* (m) by Bob Jenkins and *Kobus thomasi* (n) by Giuseppe Mazza.

III.2.4. Biome distributions

In parallel to the biogeographic analyses of forest and savanna trees (Fayolle *et al.* 2014b, 2019), I started working on the comparison between the two tropical biomes in Africa. In the frame of the post-doctoral work of Dr. Julie Aleman, we first collaborated on the distribution of forests and savannas in central Africa, which is the legacy of a long history of climate changes and human impacts (Aleman & Fayolle 2020). We used a published vegetation map for central Africa (Verhegghen *et al.* 2012) and examined the **predictions of future changes (up to 2070) of the area currently covered by forests and savannas** (including miombo woodlands). For practical reasons, the study area was defined by the boundaries of Cameroon, CAR, DRC, Equatorial Guinea, Gabon, and the Republic of Congo, covering more than 4 million km^2. According to the Tropical Rainfall Measuring Mission (TRMM, Nicholson *et al.* 2003), the environmental conditions vary widely across the study area. Mean annual rainfall ranges between 440 and 3,220 mm, from the driest sites in northern Cameroon to the wettest coastal sites also in Cameroon. Climate change-related threats are the most cited in the literature, though their impacts on tropical ecosystems are relatively unknown. Indeed, rainfall patterns are expected to change, and the probability of drought and extreme events will increase (Figure 17). Rainfall change within RCP 2.6 is expected to be less intense and extensive (1.6% of forest areas localized in the western part of central Africa) compared to what is projected within RCP 8.5 (with 62% of forests and 47% of savannas will be impacted by a decrease (or increase) in annual rainfall, with a massive drying trend over central Africa, and a localized increase in rainfall in the extreme south). The increase in croplands will have strong impacts on savannas, with an increase of more than 40,000 km² and 150,000 km² of land dedicated to crops as compared to currently in respectively RCP 8.5 and RCP 2.6 (Figure 17). The most 'optimistic' scenario in terms of emissions and radiative forcings, RCP 2.6, is projected to impact much more savanna area (14%) than RCP 8.5 (2.8%) than forest (with only 0.5 and 0.2% of their area). This large increase in croplands within RCP 2.6 is due to the increase in surface dedicated to biofuel production planned to reduce the use of non-renewable energy. During the past century, new threats have emerged for tropical biomes, as we have entered the Anthropocene (Malhi *et al.* 2014; Lewis & Maslin 2015). Apart from climate change, the alarming rates of land use change related to cropland expansion, logging concessions, and misplaced

forest plantations may represent an even more substantial threat to forest and savanna structure and composition, and ultimately ecosystem services provision.
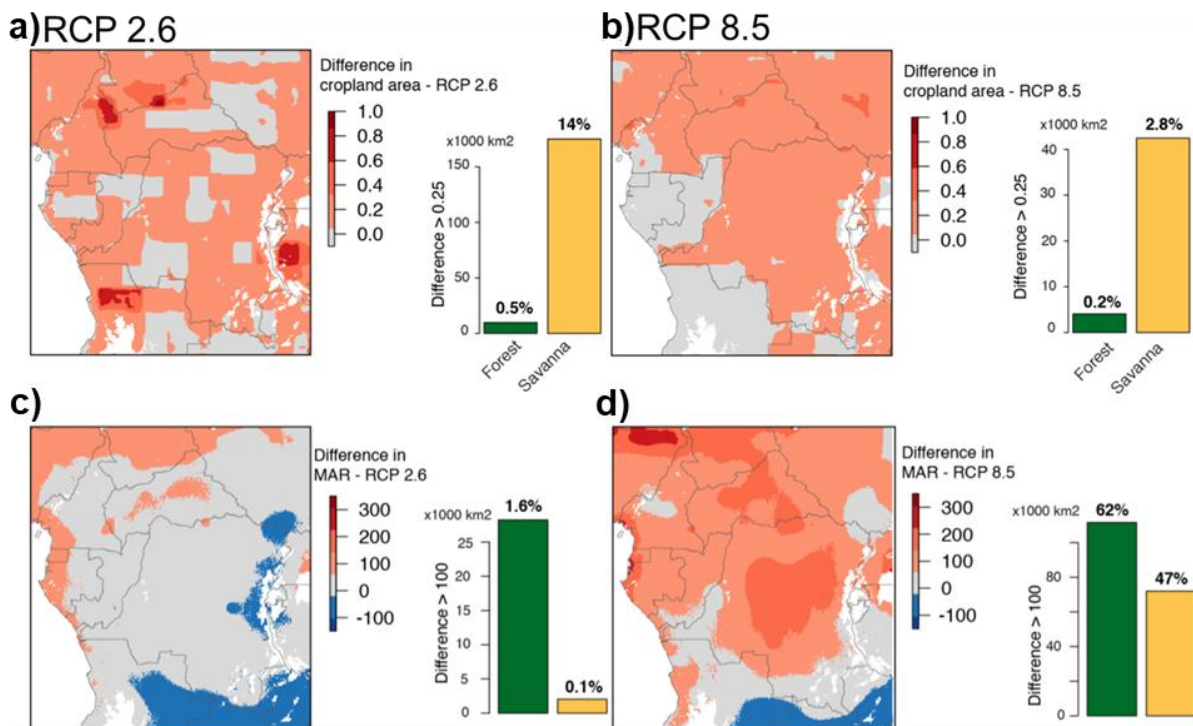

Figure 17. Predicted land-use and climate changes in central Africa. Change in cropland area and rainfall in central Africa according to RCP 2.6 (a, c) and RCP 8.5 (b, d). Change in cropland area in each pixel is estimated as the difference between current and future (in 2070) cropland area in each pixel for the scenarios RCP 2.6 (a) and RCP 8.5 (b). Barplots represent the area for which this difference is expected to exceed 25% for forest and savanna areas in central Africa. Changes in rainfall (mean annual rainfall in mm yr^{-1}) are estimated as the difference between current and future (in 2070) rainfall for the scenarios RCP 2.6 (c) and RCP 8.5 (d). Barplots represent the area for which this difference is expected to exceed 100 mm yr^{-1} for forests and savannas in central Africa. Extracted from Aleman & Fayolle (2020).

With Dr. Julie Aleman, we further collaborated on the **distribution and determinants of tropical forests and savannas distributions across (sub)tropical Africa** (Aleman *et al.* 2020). We first delimited the climatic envelope of the two biomes in Africa using the tree species lists gathered for a large number of forest (Fayolle *et al.* 2014b) and savanna (Fayolle *et al.* 2019) sites earlier mentioned. Alongside the expected patterns of forest in wetter areas and savanna in drier and more seasonal ones (Lehmann *et al.* 2011; Ratnam *et al.* 2011), also retrieved here (Figure 18a), we found an extensive climatic area (Figure 18a and b) within which both forest and savanna sites are widespread, which we term the '*bistable'* region. Mean Annual Precipitation (MAP) partly differentiates the forest, the *bistable* region, and the savanna; although the climatic gradient used to determine and map them is more complex and integrates precipitation and seasonality (Principal Component Analysis on gridded climate data). We find a large extent of forest, 1.8 million km², covering almost the whole Guineo-Congolian Region

(Figure 18c), in line with the stability of forest in Lower Guinea suggested over the last two millennia by pollen records (Vincens *et al.* 1999), but challenging previous findings of bistability across the entire Congo basin (Staver *et al.* 2011). Savanna was found to occupy most of the areas north, east and south of the Congo Basin, under drier and more seasonal conditions, and totaling almost 8.4 million km². The savanna notably includes the west coast of southern Africa (Figure 18c), which contrasts with the description of this area as thicket, scrub or bush land (White 1983). This is due to the presence of northern (Sahel) and eastern (Horn) savanna sites with extremely arid climate in the floristic surveys, which extended the climatic envelope of savanna this far, and also because northern and western savannas are not completely analogous climatically to southern and eastern ones (Fayolle *et al.* 2019).

Figure 18. Climatic envelope of the forest and savanna biomes in Africa. To determine the climatic envelopes of the two tropical biomes, the dominant climatic gradients were first identified with a Principal Component Analysis of gridded climatic variables. (a) Each point corresponds to the center of a 0.5° pixel, with pixels containing floristic surveys in forest (green) and savanna (orange) sites indicated. Red and blue arrows indicate the influence of temperature and precipitation variables, respectively. (b) Frequency distribution of forest (green) and savanna (orange) sites along a complex precipitation and seasonality gradient (PC1, a), with the climatic area where savanna and forest both occur plotted in light orange (where savanna is more common) and light green (where forest is more common). The dashed line corresponds to an equal probability of savanna and forest. (c) Map of forest and *bistable* forest, *bistable* savanna and savanna, with the locations of floristic surveys in forest (green) and savanna (orange) sites. White pixels are outside the geographic extent and/or the environmental range covered by the floristic surveys. The latter was defined by a convex hull on the site scores on PC1 and PC2 (dashed line in a). Major waterbodies and rivers are shown in blue.

Our analyses confirm extensive climatic overlap of forest and savanna, supporting the alternative stable states hypothesis for Africa, and we further find the two biomes to have highly divergent tree species compositions and to represent alternative compositional states. We

46

classified the 1,707 woody species present in at least 5 sites retained for analyses into forest (n=825) *versus* savanna (n=523) specialists, with some generalist species (n=359) that span both biomes, using the indicator value procedure of Dufrêne & Legendre (1997). In conjunction with georeferenced herbarium records made available by the RAINBIO project (Dauby *et al.* 2016), we mapped the distribution of forest and savanna specialists, and of generalist species at the scale of Africa, and we devised a biome index at the scale of 0.5° pixel which tracks the specialization of each pixel, with values toward -1 representing the dominance of savanna specialists, and values toward +1 representing the dominance of forest specialists.

$$\text{biome index} = \frac{\#sp\ for - \#sp\ sav}{\#sp\ for + \#sp\ sav + \#sp\ gen} \qquad\qquad \text{(eq. 3)}$$

where *#sp for* is the number of forest specialists, *#sp sav* the number of savanna specialists, and *#sp gen* the number of generalist species in each pixel. This allowed us to retrieve the forest and savanna distributions across Africa and quantify their environmental limits, which were found to be primarily related to precipitation and seasonality, with a secondary contribution of fire, as shown by a random forest approach. Our map of the forest and savanna distributions in Africa (Figure 1a), which consider differences in tree species composition, and a complex suite of determinants is important for the ongoing efforts to restore African ecosystems, which depend on **accurate biome maps to set appropriate targets for the restored states**. The idea that tropical forest and savanna are alternative states maintained by feedback between tree cover and disturbance, is indeed crucial to how we manage these biomes and predict their future under global change. Large-scale empirical evidence for alternative stable states is limited, however, and comes mostly from the multimodal distribution of structural aspects of vegetation (Hirota *et al.* 2011; Staver *et al.* 2011). These approaches have been criticized, as structure alone cannot separate out wetter savannas from drier forests for example (Ratnam *et al.* 2011), and there are also technical challenges to mapping vegetation structure in unbiased ways (Bastin *et al.* 2017). Here, we provided **empirical evidence for broad scale bistability**.

III.2.5. Niche differentiation

An interesting pattern in the tropical woody flora of Africa is that several genera encompass both forest and savanna species (Figure 19) as demonstrated in the early work of White (1979, 1988) on the *Diospyros* genus and that lead to the vegetation map of Africa (White 1983). In the frame of the PhD thesis of Anaïs Gorel, we investigated the evolutionary processes that allowed these lineages to adapt to contrasting environmental conditions and to cover immense areas.
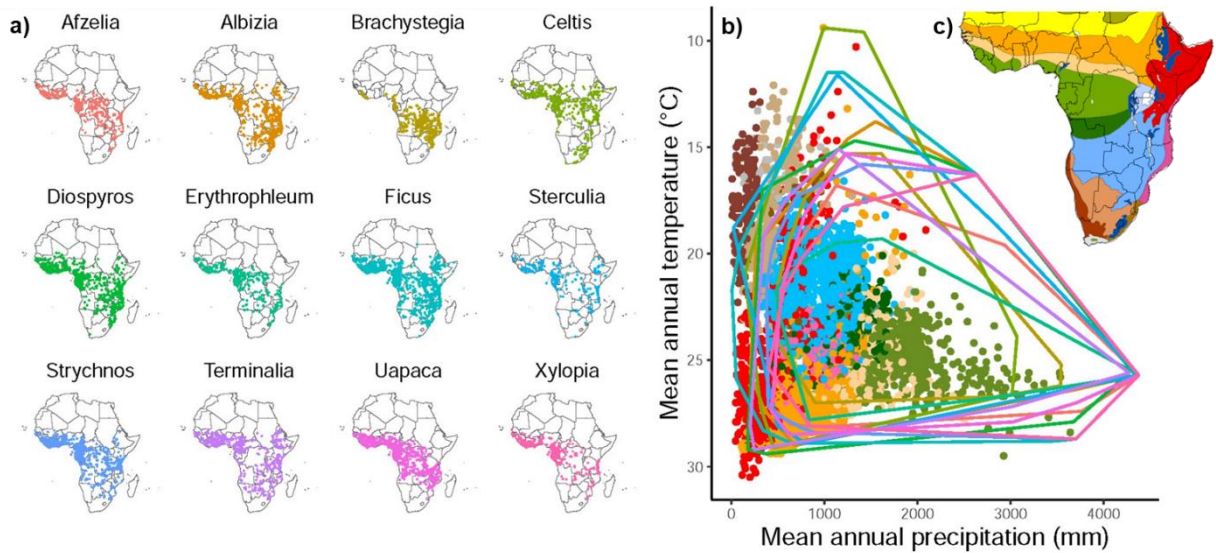
Figure 19. Tropical woody genera vastly distributed across Africa and occurring under a large range of environmental conditions. The distribution in geographical space (a) and in climatic space (b) is shown for 12 African woody genera transcending the forest and savanna boundary. Occurrence data were extracted from the RAINBIO dataset (Dauby *et al.* 2016). The background points in the climatic space correspond to the pixel covering sub-Saharan Africa according to a color code following the phytochoria, transitions zones, and regional mosaics of White (1983) shown as inset (c).

We first studied **niche differentiation** within a specific lineage, the *Erythrophleum* genus (Fabaceae) in Africa. We examined the extent of niche differentiation between the four congeneric species found in Africa (Gorel *et al.* 2015, 2019a) and studied in-depth the two forest species which are very similar morphologically and sold under the same commercial name, Tali, but show adjacent distributions along a rainfall gradient (Figure 20a). *E. ivorense* is a wet forest species and *E. suaveolens* occurs in moist forest and forest gallery as shown by genetic data (Duminil *et al.* 2010). We implemented an ecophysiological approach to identify the functional changes associated with niche evolution. Using *in situ* measurements on adult trees, we first examined between-species differences in stem hydraulics including vulnerability to embolism, wood water content and capacitance, and we determined the underlying wood traits, especially vessel-associated traits. Measurements were done on fresh stem and branch samples collected in two sites representative of the natural habitat of the two species, the Ma'an and Mindourou sites, earlier mentioned in the work on allometry. The branch samples were kept watered during transport up to the laboratory of Plant Ecology in Ghent University (Belgium) for the hydraulic measurements and both stem and branch samples were used for measurement of wood anatomical traits in the wood biology service of the Royal Museum for Central Africa in Tervuren. Growth was quantified from tree monitoring on permanent paths in Ma'an and Mindourou. Data and samples from a common garden in Mindourou were also used to test whether differences in growth and wood traits observed in the natural habitat are maintained under the same

environment. In addition, we designed a controlled experiment to examine the effects of drought on leaf gas exchange of one-year old seedlings of the two forest species. We measured leaf gas exchanges and plant water status of control (well-watered) and drought-stressed (water-withheld) seedlings over time in the green-house of the Laboratory for Plant Ecology of Ghent University. Combining these approaches, 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* (Gorel *et al.* 2019b). The specialization to drier environment of the moist 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 embolism (Figure 17c).
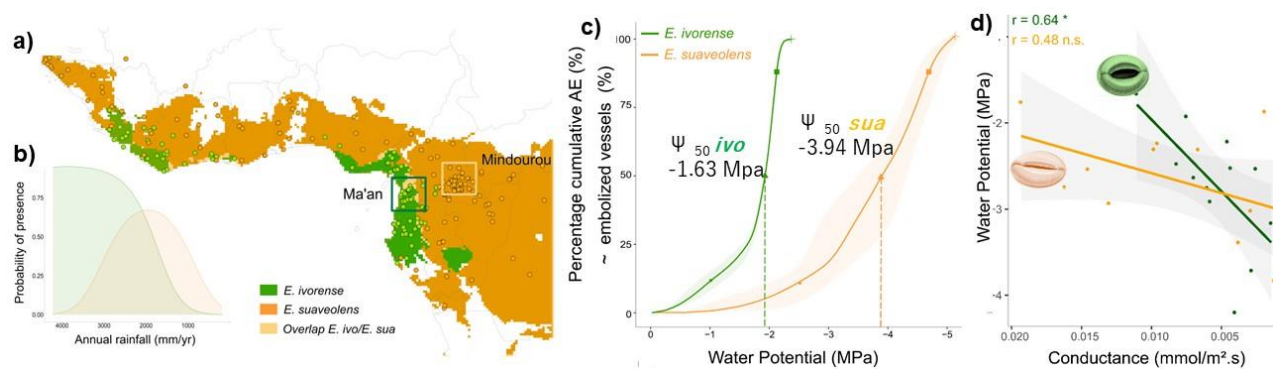

Figure 20. Niche and trait differentiation between sister species. Potential distribution in Upper and Lower Guinea (a) and response curve (probability of presence) along the rainfall gradient (b) of the two sister species *Erythrophleum ivorense* (in green) and *E. suaveolens* (in orange). The average rainfall has been extracted from "bioclim" data (BIO12, Hijmans *et al.* 2005). The distribution of *E. suaveolens* is much larger across southern and eastern Africa, but genetic information was lacking (Duminil *et al.* 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, is indicated on the map (colored squares). The common garden experiment was set up at the Mindourou site, that is, in the natural habitat of *E. suaveolens*. The occurrence data used to model the distribution of the species overlaid on the map. The potential distributions and the response curves result from species-specific distribution modeling. See Supporting Information Appendix S1 of Gorel *et al.* (2019b) for a description of the methods used. (c) Stem hydraulic traits, and specifically acoustic vulnerability curves for the wet forest species *E. 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) were obtained by plotting cumulative AE values against xylem water potential. The vulnerability thresholds AE12 (circle), AE50 (triangle), AE88 (square), and AE100 (cross) are indicated as well. (d) Mean water potential over mean conductance measured on drought-stressed (water-withheld) seedlings over time during for *E. ivorense* (green) and *E. suaveolens* (orange). For each species, Pearson correlation coefficients and significativity (n.s: $P>0.1$, -: $P<0.1$, *: $P<0.05$, and ***: $P<0.001$) were shown on graphs and linear smoothing (±SE) were used to highlight anisohydric-isohydric trends.

Our seedling experiment showed that two desiccation delay-strategies contributed to delay a fall in xylem pressure during drought: 1) an early stomatal closure, limiting water loss trough transpiration (Figure 17d), and 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. 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, and wood traits allowing high hydraulic efficiency. 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, allowing a constant transport of water for photosynthesis, while avoiding catastrophic embolism formation.

In the frame of the post-doctoral work of Anaïs Gorel at Gent University under the supervision of Kathy Steppe, we extended our analyses of niche evolution at a larger scale in a recently published study (Gorel *et al.* 2022). Specially, we characterised the climatic niche of >4,000 tropical African woody species including trees, shrubs and lianas, using the approach of Broennimann *et al.* (2012) and the niche comparisons among species allowed distinguishing two broad bioclimatic groups (forest *versus* savanna) and six climatic subgroups. We quantified **biome conservatism versus lability** at the genus level and for higher clades, using a molecular phylogeny of >800 genera (Segovia *et al.* 2020), with species branched as polytomies. Although biome stasis at speciation was found to be prevalent, numerous clades individually cover vast climatic spaces, as shown earlier for specific genera (Figure 19), suggesting a general ease in transcending ecological limits. The forest biome was the main source of diversity, providing many lineages to savanna, but reverse shifts also occurred (Figure 21).
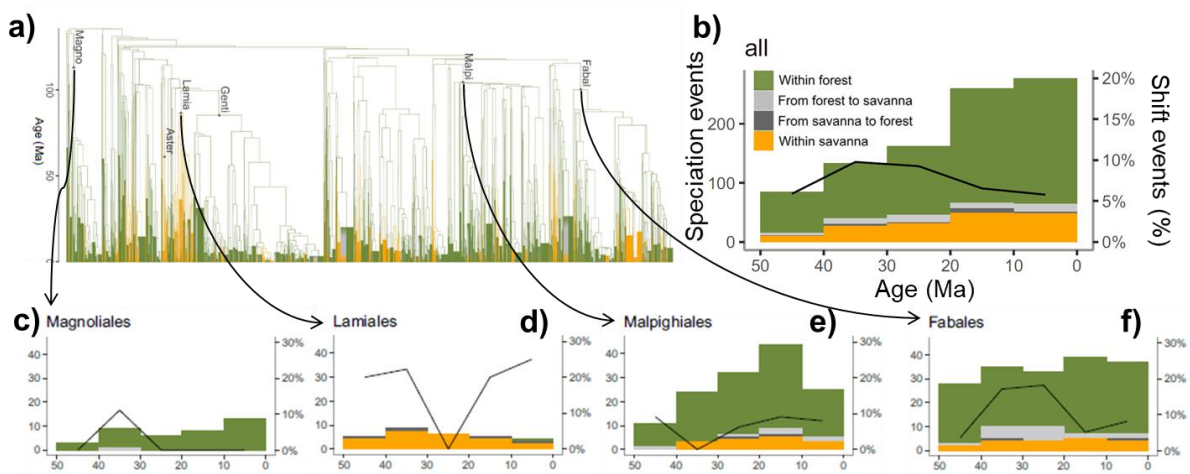

Figure 21. Biome lability across time. Ancestral biome was reconstructed (a) for woody Angiosperms. The tree was colored according to the most likely states of nodes: forest (green) or savanna (orange) and some ancestral nodes corresponding to taxonomic orders were highlighted. The timing of speciation events and shifts since 50 Ma was assessed for all lineages (b) and four highly diversified orders (c-f). The bars represent the number of speciation events on our phylogeny (left axis) and the line represents the percentage of speciation events associated with biome shifts (right axis).

Additionally, we explored whether the forest-savanna transition was consistently associated with a growth form change (*i.e.*, liana, shrub, tree), and though we found evolutionarily labile clades whose presence in forest or savanna is associated respectively with climbing or shrubby species diversification, overall growth form appeared highly conserved.

III.3. Tropical forest and tree functioning

III.3.1. Data needed for forest management

I have precised quite early in this manuscript that my work is anchored into applied forest sciences and that the data that have been accumulated to answer practical questions have also helped answer more fundamental questions in ecology. Moving back to the practical implications, the information needed for the sustainable management of timber species in production forests are related to (i) **species diameter at reproduction** which is used to adapt the minimum cutting diameter (the diameter above which the species can be exploited) and which guarantee that seed trees are left after logging; to (ii) **species growth and mortality rates** that are used in the computation of the recovery rate (Durrieu De Madron & Forni 1997) at second rotation, and to (iii) **accurate volume equations** that are used to divide the forest concession into annual cutting areas of equal volumes, and then yearly to plan exploitation and sale the exploited volumes. The forest administrations in each country grant the logging concessions for a certain time, and define the management rules, which includes the cutting diameter of species, their growth and mortality rates, and the volume equations to be used. The latter point concerning the suitability of volume equations needed destructive measurements for a precise estimation of tree volume and has been addressed in the tree allometry section but for assessing the reliability of cutting diameters, and growth and mortality rates, imposed by forest administrations, **tree monitoring in the field** is needed.

For monitoring tree growth and mortality, different kind of sampling approaches have been implemented in central Africa (Picard & Gourlet-Fleury 2008). In **permanent sample plots** of one-hectare and beyond, all trees above a certain diameter threshold (10 cm in diameter in general) are localized in the plot, identified to species and their diameter is measured at a certain height corresponding to breast height (1.30 m) when the stem is regular and above deformations (30 or 50 cm) when present. The Point of Measurement (POM) is painted on the tree to guarantee re-census of diameter at the same height. Over the successive re-census of the trees, it is possible to compute growth (*i.e.*, annual diameter increment) at the tree level, and

mortality and recruitment rates at the population level. Given the extremely low stem density of some timber species and the need to capture the species diameter range, another type of sampling has been proposed and implemented in logging concessions, the **path approach** ('sentiers' in French). Trees belonging to the timber species targeted by the logging company are selected, and when possible 20 trees by 10-cm wide diameter class from 10 cm and up to the minimum cutting diameter are localized in the field. Since these trees are generally also monthly monitored for phenology, a path is formed in the forest understory, connecting all these trees. In the DynAfFor project and its second phase, the P3FAC project, both plots and paths were installed in the same sites so that to benefit from both sampling strategies, to have growth and mortality of timber species well monitored in the paths, and to be able to compute recruitment from the plot data, the latter are also used to describe the forest stand structure and diversity. In addition, plots and paths were both installed in a control treatment (that will be never logged) and in a logged treatment, during which trees are measured before and after logging, forming a BACI (Before After Control and Intervention) sampling design. I was personally involved in the installation and monitoring of the plots and paths installed in the Bambidie site (CEB Precious Woods logging concession) in Gabon. The plots were installed in 2019, and I supervised the master's thesis of Yorick van Hoef during which we selected the location of the 8 4-ha plots based on a pre-inventory of the area targeting 40 timber species over the whole north (blue) and south (red) blocs (Figure 22).
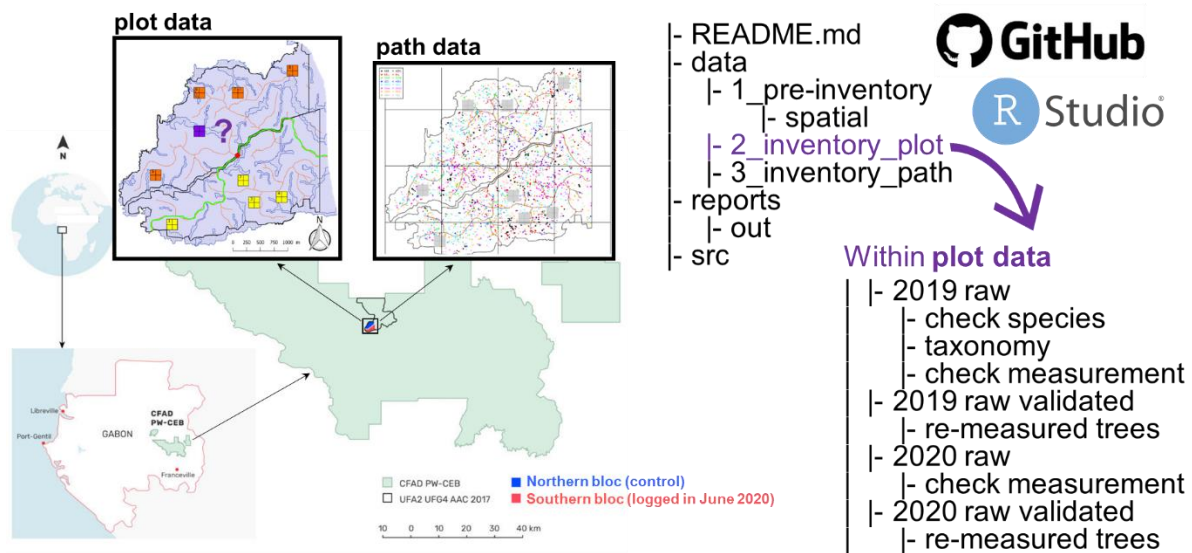

Figure 22. Management of forest dynamics data. Permanent sample plots and paths were installed in Bambidie (CEB Precious Woods logging concession) in Gabon in the frame of the P3FAC project. The management of these data is based on a GitHub project shared by Adeline Fayolle and Gauthier Ligot, respectively for the plot and path data. The northern part of the study area (in blue) corresponds to the control block while the southern parts (in red) has been exploited for timber in June 2020. In June 2022, a

recensus is planned to complete the installation (2019) and the first census (2020), and so will be every two years.

I also used the information of this pre-inventory to select the trees forming the path, after having selected the species to be monitored with the manager of the logging company, Philippe Jeanmart, and my colleague Jean-Louis Doucet. I also supervised the master's thesis of Stévy Nna Ekoné in 2019 who finalized the installation of the plots and of the paths. My colleague Gauthier Ligot is now in charge of the path data while I continue supervising the plot data (> 12,000 trees that will be remeasured this summer). The southern bloc (in red on the map of the concession, and the yellow plots) have been exploited in June 2020 and a first census was made in July-August 2020 to quantify the immediate impacts of exploitation. We have tried using direct encoding on smartphones adapting OpenForis formularies which appeared suited for the recensus of the trees in the paths and not very efficient for that in the plots.

III.3.2. Tree performance

I was involved in several studies related to tree and species performance though I am not an expert of forest dynamics. Maximum growth observed in the M'Baïki experiment were provided in the study of Gourlet-Fleury *et al.* (2011) and related to species affinity with the soil type, and notably the resource-poor soils found on the Carnot sandstone. In the work of Richard Fétéké who was a forest manager at Pallisco CFIM logging company in Cameroon, we showed that the tree growth values currently used in Cameroon for computing stock recovery over the rotation cycle during management planning are not different from those observed in undisturbed forests for Assamela, Moabi and Tali, but they overestimate the growth of Sapelli by 20% (Fétéké *et al.* 2015). Growth models were also fitted for these four species including competition which was measured in the field in a 20-m radius circular plot around each target tree. A potential × reductor modeling approach was adopted and the log-normal model selected well described the hump-back shape of the relationship between tree diameter and diameter increment previously observed, in French Guiana notably (Herault *et al.* 2011). In contrast, the diameter increment of Ayous (*Triplochiton scleroxylon*) was found to be only weakly related to tree size as shown in the age estimation process of our earlier study (Morin-Rivat *et al.* 2017) but increased twofold from unlogged to logged forests (Figure 23).
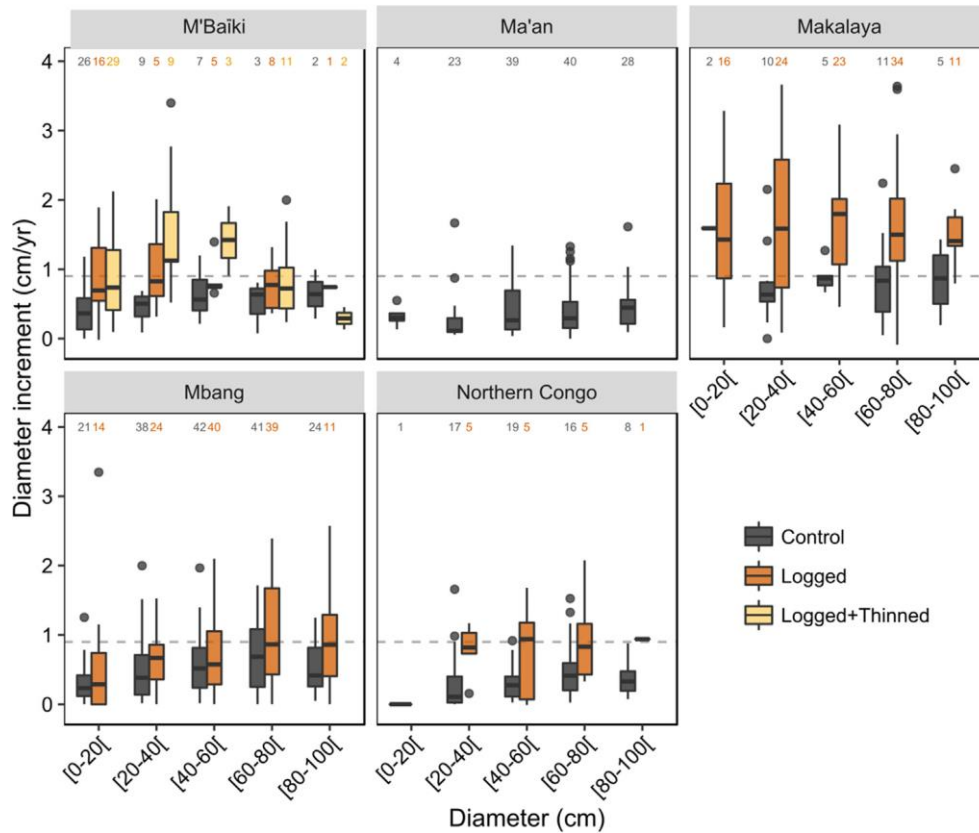
Figure 23. Growth variation of *T. scleroxylon* across sites and logging treatments. The dashed horizontal gray line indicates the diameter increment (0.9 cm yr⁻¹) as fixed by the Cameroon government for the calculation of stock recovery rate. Numbers indicate the sample sizes for each boxplot.

In the frame of the post-doctoral work of Gauthier Ligot, a vast amount of tree diameter observations, 13,225 records of annual tree diameter increments recorded over 920 trees were compiled and analyzed. Our results shows that the diameter increment of this species is remarkably variable in unlogged forests ranging between 0.40 cm yr⁻¹ southern Cameroon and 0.83 cm yr⁻¹ in south-eastern Cameroon, and growth stimulation caused by logging last at least 10-15 years (Ligot *et al.* 2019). The same kind of analysis was conducted for 42 timber species across central Africa in the frame of the DynAfFor/P3FAC projects (Ligot *et al.* 2022). I was not involved in this study, but it is important to note that growth stimulation due to logging tended to be lower for the other species. In contrasts, I oversaw the data analyses of growth and mortality of 23 timber species in plantations (Doucet *et al.* 2016) in which we also find a lot of variability for Ayous. I was also involved in two studies analyzing species performance in silvicultural trials that were installed in the field by Jean-Louis Doucet and his students (Ouédraogo *et al.* 2014; Fayolle *et al.* 2015).

III.3.3. Phenology

In the path design, trees are monitored once a year for growth and usually monthly for phenology. **Size at reproduction** is a key aspect of species life history that is relatively understudied for long-lived tropical trees and knowing size at reproduction is also important to define minimum cutting diameter limits (MCDL) that ensure that seed trees are left after logging (below the MCDL, Durrieu De Madron & Daumerie 2004). I was first involved in a study of the size at reproduction for the Wengé, *Millettia laurentii* (Fabaceae) in three logging concessions of the DRC (Menga *et al.* 2012), and then for 31 major timber species across 11 sites in Cameroon, Congo, and CAR (Ouédraogo *et al.* 2018) and 13 tree species in the Luki site in the DRC, thanks to the historical data (Angoboy Ilondea *et al.* 2019). A great **variability in diameter at reproduction** was found among species, which correlated with adult stature (Ouédraogo *et al.* 2018), consistent with studies conducted elsewhere in the tropics (Thomas 1996; Davies & Ashton 1999; Wright *et al.* 2005; Thomas *et al.* 2015). For some species, reproductive diameter thresholds substantially varied between sites, and crown exposure had a significant positive effect on reproductive status, as observed for the Wengé (Menga *et al.* 2012), confirming the **important role of light availability for tropical tree phenology** (Wright & Van Schaik 1994). We found that most MCDLs imposed by national forest regulations enable seed trees to persist after logging operations though MCDLs might remain questionable for some species, notably for *Erythrophleum suaveolens* and *Triplochiton scleroxylon*, the latter being recognized for long for its irregular reproduction.

The phenological data of the M'Baïki site, and notably the last monitoring period since 2005 for which 14 timber species were monitored every two weeks, was included in the first cross-site analysis of tree flowering across tropical Africa (Adamescu *et al.* 2018) that demonstrated that annual cycles are widespread and dominates in most sites (Table 4), using the Fourrier transform approach earlier proposed (Zalamea *et al.* 2011; Bush *et al.* 2017). The **dominance of annual phenological cycles** was also retrieved in specific sites, such as Lopé NP in Gabon (Bush *et al.* 2017) and Luki in DRC (Angoboy Ilondea *et al.* 2019), and is probably attributed to the lower rainfall of tropical forests in Africa (Guan *et al.* 2015) which also experience higher seasonality in comparison with the other tropical regions.

Table 4. Dominance of annual phenological cycles in tropical Africa. The number of individual trees and species monitored for phenology at each African site in the original and Fourier datasets. Fourier analyses were used to identify the dominant cycles of flowering and fruiting for each individual tree. Reproductive strategies were diverse, and no single regular cycle was found in >50% of individuals across all 12 sites, but annual flowering (and fruiting, results not shown) cycles were the most common. Extracted from Adamescu *et al.* (2018).

			Detected cycle sample		Characteristics of detected cycles					
					Sub-annual		Annual		Supra-annual	
	Original sample									
Site (Southeast to northwest)	N Species	N trees	N Species	N trees	N Species	N trees	N Species	N trees	N Species	N trees
Amani	70	935	14	410	14	252	7	23	14	135
Gombe	13	277	11	192	7	13	10	146	7	33
Nyungwe	74	1000	45	794	35	187	43	326	42	245
Bwindi	33	319	8	80	6	40	6	18	8	22
Kibale	75	311	10	85	8	29	7	13	10	43
Okapi Lenda	49	570	27	354	17	60	27	251	19	43
Okapi Edoro	61	850	30	439	27	111	24	140	29	188
M'Baïki	30	769	6	155	6	55	5	36	6	64
Goualougo	28	284	3	43	2	19	3	20	1	4
Mbeli	44	438	12	112	10	24	11	55	11	33
Lope	84	940	48	733	33	167	45	478	30	88
Taï	108	1000	44	2049	43	663	43	973	39	413
Total	669	7693	258	5446	208	1620	231	2479	216	1311

While land surface phenology studies are difficult to implement in central Africa because of cloud cover (Adole *et al.* 2016), satellite observations nevertheless showed that **forest functioning is highly seasonal** and the bimodal pattern retrieved for vegetation indices mimics rainfall seasonality with two peaks corresponding to the wet seasons, notably in the Sangha River Interval (Gond *et al.* 2013) and across central Africa (Philippon *et al.* 2019). In these two studies, I helped the remote-sensing scientists and climatologists interpreting the spatial and temporal patterns retrieved. In addition, an interesting feature of the African continent is that tropical forests occur on both side of the Equator (Figure 18) with a **six-month delay in seasonality** between northern forests with a long dry season in January-February and southern forests with a long dry season in July-August (Figure 12). A phenology shift was suspected approximately located ~ 2°N of the Equator to explain the genetic diversity patterns observed within tree species, this area indeed corresponds to the limits of genetic clusters for many tree species (Hardy *et al.* 2013) and this is also the area where the dry season reverse. We tested this hypothesis with phenology information derived from herbarium specimens for eight timber species (Figure 24) and we only found a **shift in the timing of flowering** with latitude for *Erythrophleum suaveolens*, and with the timing of the dry season for *Milicia excelsa* (and to a lesser extent *Lophira alata*), with the coexistence of two flowering peaks near the Equator where the distribution of monthly rainfall is bimodal (Ouédraogo *et al.* 2020).
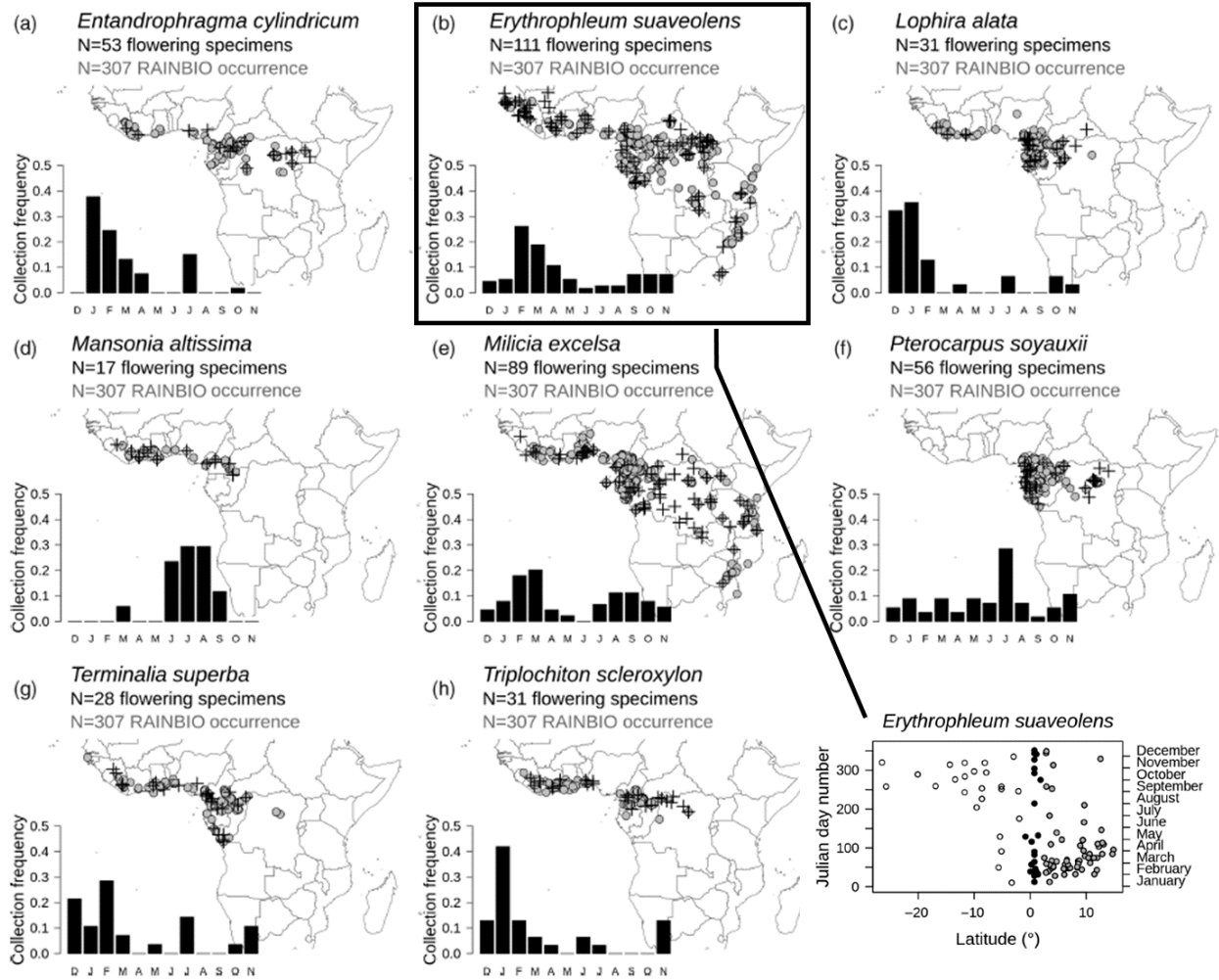
Figure 24. Test of the phenology shift across the Equator. Location of flowering herbarium specimens (black crosses, number N indicated in black) across Africa for the eight study species. Species spatial distribution, *i.e.*, location of RAINBIO occurrences (Dauby *et al.* 2016) is indicated with grey circles (number N indicated in grey). Insets show the frequency of flowering herbarium collections by month (represented from December to November for clarity). The relationship between calendar dates of flowering herbarium specimens (in Julian days) and latitude is shown for *Erythrophleum suaveolens* as inset. Open circles represent specimens collected at south of 1°S, black circles those collected between 1°S and 2°N, and grey circles those collected at north of 2°N. For clarity, the second y-axis indicates the months corresponding to Julian days.

Chapter IV. Research perspectives

IV.1. Research priorities

Here, I finally propose a research project on forest and tree seasonal functioning, and response to drought. While deforestation and forest degradation remain the top human threats on tropical forests (Malhi *et al.* 2014; Vancutsem *et al.* 2021), climate is expected to progressively shift to drier conditions in the tropical belt, adding an extra pressure on the system with large-scale die-back of tropical trees already observed in the Amazon (Phillips *et al.* 2009). The situation might be even more alarming in Africa, where climate is already drier and more seasonal than in the other tropical regions, with the vast majority of African tropical forests occurring below the climatic threshold of approximately 2,000 mm.yr^{-1} annual rainfall identified for maintaining dry season canopy photosynthesis in tropical forests worldwide (Guan *et al.* 2015). In addition, future conditions in Africa (Figure 25) have no climate analogues today, leading to important uncertainties about how trees, species and communities will cope with the drier conditions predicted by climate models (Greve *et al.* 2014). Changes in climate are expected to be strongest in the dry/arid regions (Platts *et al.* 2015), but on-site data in central Africa shows an already significant drying trend in Lopé NP, Gabon (Bush *et al.* 2020a) while in west Africa a drought-induced shift in forest species composition has already been observed (Fauset *et al.* 2012) and more intense shifts have been reported at drier sites (Aguirre-Gutiérrez *et al.* 2019).
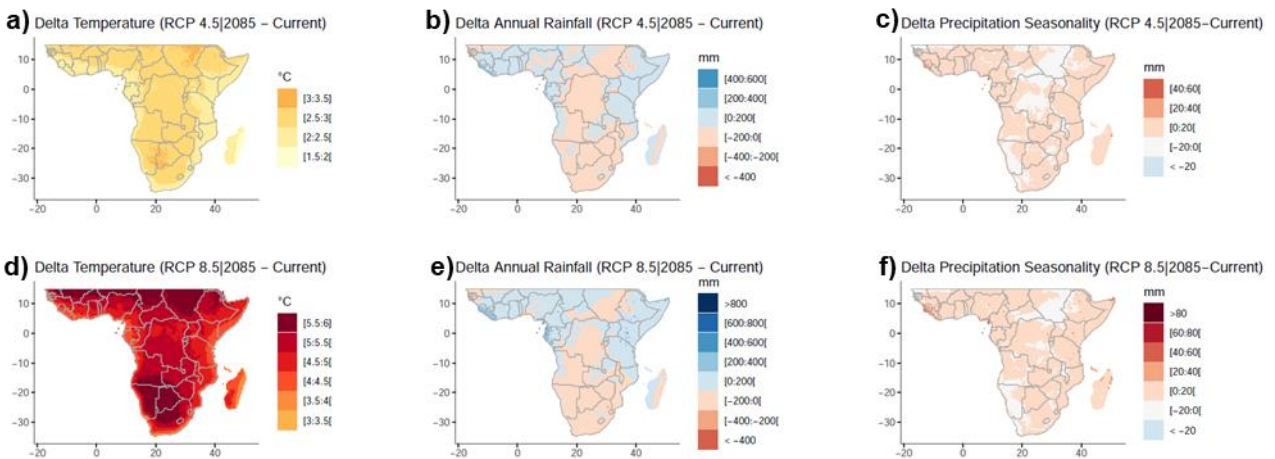

Figure 25. Extent of climate changes across sub-Saharan Africa predicted by RCP 4.5 (a-c) and 8.5 (b-d). The difference (delta) between predictions for the year 2085 and the current observations are shown for temperature (a and d), annual rainfall (b and e), and precipitation seasonality (c and f).

Whether tropical forests in central Africa will be sensitive to drier conditions –because trees are already limited by water availability– or resistant –because species are adapted to seasonal drought– is on the top list of research priorities in tropical and global change ecology. This is also the ambitious challenge we aim to tackle in a research project entitled **CANOPI** (Central African Network of Observatories of troPIcal tree and forest functioning) that has been recently funded by the Excellence Of Science (EOS) joint call of the Walloon (FNRS) and Flemish (FWO) research agencies in Belgium. Our consortium is composed of two Belgian universities, the University of Liège in Wallonia (with Adeline Fayolle as PI and Jean-François Bastin as co-supervisor), and the University of Gent in Flanders (with Kathy Steppe as PI and Wannes Hubau as co-supervisor), and two southern partners, the CENAREST in Gabon (with Alfred Ngomanda as PI and Katharine Abernethy as co-supervisor), and the INERA in the DRC (with Bhély Angoboy Ilondea as PI). To resolve the major uncertainties in the resilience assessment of central African forests to climate change, we will use a pioneering and transdisciplinary approach. Specifically, we will address four pressing fundamental scientific questions (SQ) in specific work packages (WP) with a fifth WP dedicated to upscaling (Figure 26).

SQ1. To what extent does and will climate, and specifically seasonal drought, shape tropical tree species distribution in Africa? We will determine the potential distributions of numerous forest species under current and future climates and highlight the environmental determinants shaping their distribution. We will use Species distribution modelling (SDM) that has long been recognized as a powerful tool to predict distribution ranges of biological entities in time or space by relating occurrence data to environmental gradients (Guisan & Thuiller 2005). We will use occurrence data available from herbarium records (Dauby *et al.* 2016) and checklists (Fayolle *et al.* 2014b, 2019) and different environmental layers. Using climate predictions, we will identify threatened species as well as areas that will experience major shifts in taxonomic and functional composition. In addition, recently published angiosperm phylogenies at genus (Segovia *et al.* 2020) or species (Janssens *et al.* 2020) levels will be used to quantify the phylogenetic signals in species distribution and traits. Trait data will be compiled in the other WPs of the project (maximum height, light requirement derived from crown exposure to light, presence of green tissue on the stem or branches) and complement with existing information from the literature (leaf phenology, dispersal mode, wood density, etc.). We will specifically explore the role on species distribution of drought-related traits, such as a deciduous leaf habit, given the importance of phenology for species distribution (Chuine 2010), and using phylogenetic information, we will test whether the evolution of these traits within lineages is related to niche shifts towards drier climates.
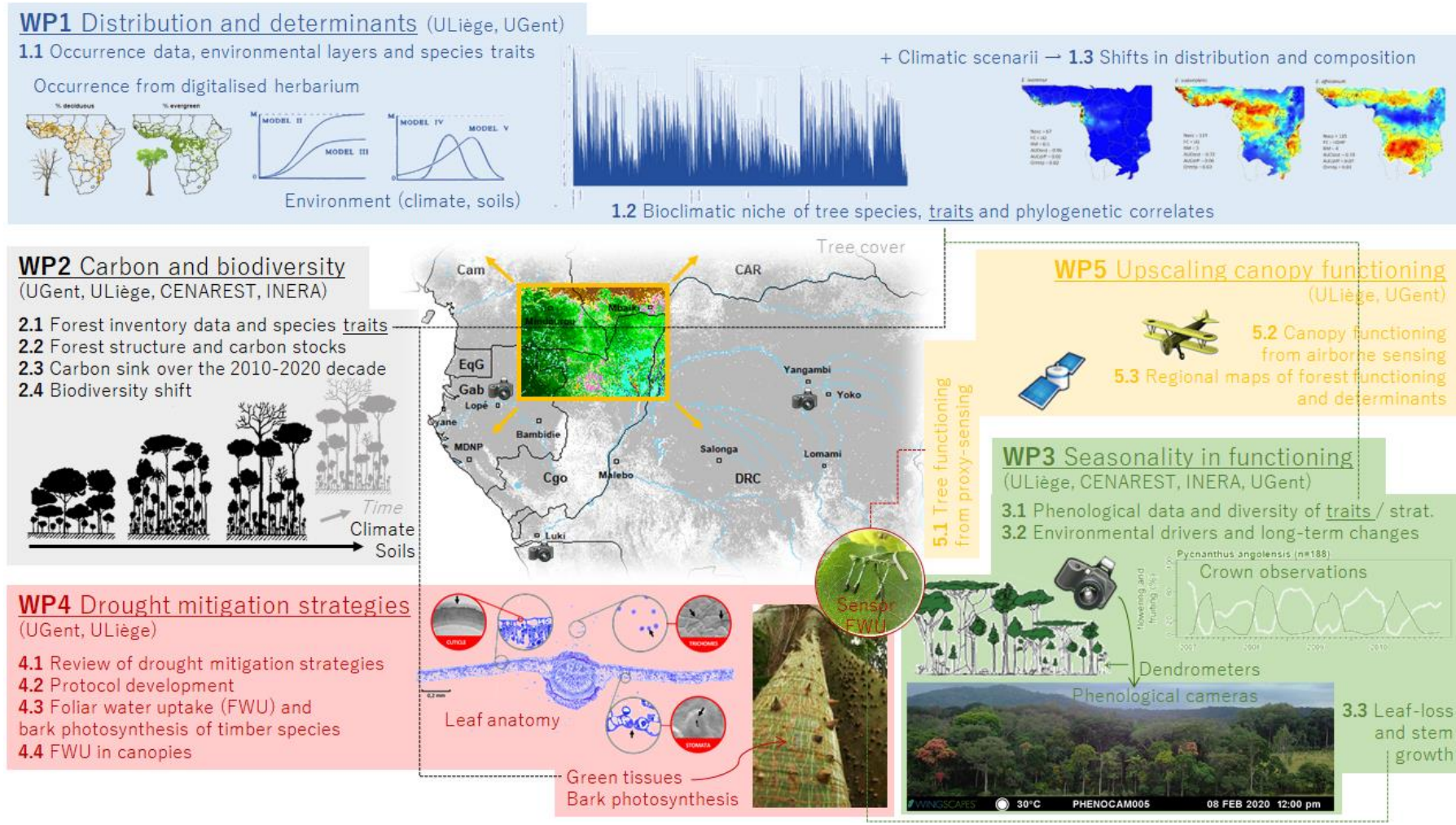
Figure 26. Outline of the CANOPI project. The CANOPI project is based on a Central African Network of Observatories of troPIcal tree and forest functioning. The work packages (WPs), tasks (numbered), and synergies, and key roles of the consortium team members (between brackets) are shown. Spatial and temporal scales are illustrated, as well as the field sites.

SQ2. Which forests in central Africa are carbon sinks or sources, and which (type of) species are declining or currently favoured? It has been recently demonstrated that intact forests in the Inner Congo Basin represent substantially lower carbon stocks than other tropical forests in Africa, because of a specific height-diameter allometry (Kearsley *et al.* 2013). We will extend this important analysis and test the hypothesis of contrasted allometry and carbon stocks for evergreen and deciduous forests (Fayolle *et al.* 2016). We will also test the hypothesis that despite their lower carbon stocks, forests in the inner Congo basin might sequester more carbon because of a more dynamic system compared to Atlantic central African forests (Hubau *et al.* 2020). Finally, because forest compositional changes have already been reported in the Amazon (Esquivel-Muelbert *et al.* 2019) and west Africa (Fauset *et al.* 2012), the latter in favour of deciduous tree species, we will test the hypothesis of an ongoing shift in composition in central Africa as climate is changing, as shown in Lopé NP, Gabon (Bush *et al.* 2020a). It will be possible to assess changes in carbon and biodiversity because we will re-measure permanent sample plots. This might seem a simple and old-fashioned technology, but it has sparked a series of modern revolutions in tropical ecology allowing to '*take the pulse of Earth's tropical forests*' (ForestPlots.net *et al.* 2021). We will specifically focus on nine clusters of plots well distributed across the undersampled inner Congo basin and in Atlantic central Africa to evaluate the differences in forest structure, composition and dynamics between the two regions (Table 5), and to perform additional measurements and observations at the tree level that will allow deriving traits at the species level.

Table 5. Metadata of the selected plot clusters that will be re-censused in the frame of the CANOPI project (see map in Figure 26 for precise location).

Plot cluster	Total area (ha)	Installation period	Censuses	Manager within the CANOPI consortium
Inner Congo basin				
Yangambi (DRC)	22.5	2012	4	W. Hubau
Yoko (DRC)	24	2009	4	W. Hubau
Salonga (DRC)	17	2008	3	W. Hubau
Lomami (DRC)	18	2015-2018	1	A. Fayolle, W. Hubau
Malébo (DRC)	32	2013	1	J-F Bastin
Atlantic central Africa				
Luki (DRC	19	2009	3	B. Angoboy Ilondea
Bambidie (Gabon)	32	2019	2	A. Fayolle
Lopé (Gabon)	15	1987-1993	3	K. Abernethy
Oyane (Gabon)	34	1987	2	A. Ngomanda

SQ3. How does seasonal drought affect the functioning of trees and forests in central Africa? Using an unprecedented dataset of tree crown observations from the ground, we will test the dominance of annual cycles at the species and the tree level, which has so far only been demonstrated at the site level with flowering (Adamescu *et al.* 2018). We will also examine the diversity of phenological patterns across central Africa since a myriad of phenological strategies have been reported, ranging from continuous flowering/fruiting, over regular (either annual or sub-annual) and irregular phenological patterns, including supra-annual phenology and mast events (Newstrom *et al.* 1994; Sakai 2001; Norden *et al.* 2007). We will also assess how seasonal and long-term variations in key environmental factors act as cues and/or drivers for these phenological patterns, integrating between-site variations. Seasonality in functioning will also be investigated with the acquisition of new high-frequency data in key sites using state-of-the-art, easy-to-implement and robust approaches, combining crown observation of leaf loss with phenological cameras, *i.e.,* PhenoCams, and radial stem growth with dendrometers on the same trees (Angoboy Ilondea *et al.* 2021). We will specifically test the hypothesis that climate seasonality has an ultimate (adaptation to seasonality) rather than a proximate (immediate environmental cue) control, as earlier shown in south African woodlands (Ryan *et al.* 2017).

SQ4. Which drought mitigation strategies are used by the canopy tree species? We hypothesize that foliar water uptake (*i.e.*, absorption of atmospheric water directly into leaves) and bark photosynthesis (*i.e.*, carbon fixation by photosynthetic, green bark in woody tissues) will contribute to drought mitigation of canopy trees. If these mechanisms are indeed common strategies that have been overlooked, they may have a profound impact on seasonal functioning, and on the cycling of carbon and water.

A PhD position will be attributed to each WP and a transversal post-doctoral fellow working on traits will help coordinating research activities. The latter position is central to the project and will require a very skilled post-doc as noticed by the reviewers of the proposal. However, as a consortium we had the chance and opportunity to train such a person in the past years, Dr. Anaïs Gorel, and she will be available for the project, after her contract at Gent University under the supervision of Kathy Steppe. The ideas behind the development of the CANOPI project indeed rooted in the PhD thesis of Anaïs Gorel during which the collaboration with Kathy Steppe started. Below, I detail some research perspectives I personally have on the seasonal functioning of trees and canopies (WP3) illustrated with ongoing work (unpublished results).

IV.2. Seasonality in functioning

Long-term phenological data from 12 sites across tropical Africa were previously analysed at the site level (Adamescu *et al.* 2018) and the five sites located in central Africa (Lopé NP in Gabon, M'Baïki in CAR, Mbeli and Goualougo in Congo, Okapi-Lenda and Okapi-Edoro in DRC, Table 4) could be further used to compare reproductive strategies for > 200 tree species. These data will be complemented with phenology surveys of timber species in logging concessions (Ouédraogo *et al.* 2018) and historical surveys from the colonial era for the Luki site in DRC (Angoboy Ilondea *et al.* 2019) and possibly for the Yangambi site also in DRC (http://junglerhythms.org/data/visual/). Data owners have been contacted and data sharing agreements have already been signed for some sites in the frame of a PhD thesis co-supervised by Katharine Abernethy and me, but the student resigned after one year. Using complementary approaches, including graphical observations to categorize phenological patterns (Newstrom *et al.* 1994), Fourier transform analyses to determine the dominant periodicity of phenological cycles (Zalamea *et al.* 2011; Bush *et al.* 2017) and circular statistics to determine the strength and calendar date of phenological peak for one-year cycles (Davies & Ashton 1999; Morellato *et al.* 2010), we will describe the **diversity of phenological strategies among coexisting species**. At the species level, we will test the hypothesis that annual cycles dominate and we will determine the dominant season for flowering/fruiting, since timing and environmental control on reproductive phenology is likely species-specific (Wright & Calderón 2018) and associated with specific traits (Sun *et al.* 1996). The links with traits from literature and derived from measurements/observations in plots (WP2 of CANOPI) and the features of species distribution (optimum and breadth, from WP1 of CANOPI) will specifically be examined.

We will identify the **environmental drivers of phenology** at the site and the species level. We will specifically test the relative importance of light (Wright & Van Schaik 1994) and water (Borchert 1994) availability using on-site data and/or appropriate remote-sensing products for meteorological data (rainfall, temperature and irradiance, Philippon *et al.* 2019) and new modelling approaches will be investigated (Wright & Calderón 2018). Under seasonal climate, strong constraints on phenology are expected, leading to phenological synchrony among species (Borchert *et al.* 2004). Peaks in reproduction in the rainy season might reduce drought stress on reproductive adults and seedlings, however, phenological surveys in seasonal forests tend to show the opposite trend, with leaf-flushing and flowering occurring mostly during the dry season (Frankie *et al.* 1974), and this is the trend we also observe in the M'Baïki site at the northern margin of the Congo basin forests, with a flowering peak during or at the end of the long dry season (DJF) and with leaf loss preceding flowering for deciduous species (Figure 27).
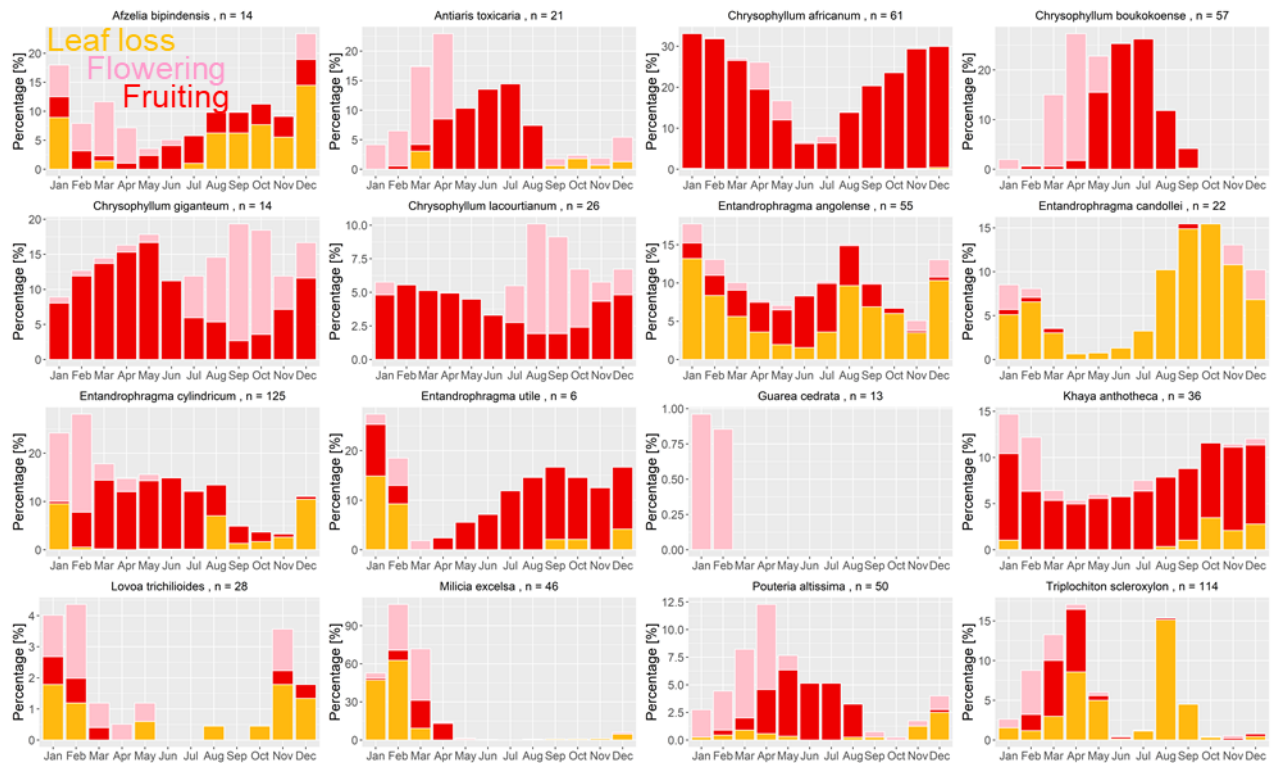
Figure 27. Seasonal variation of tree phenological status. The monthly average of the percentage of trees in the three phenological status recognized in the M'Baïki (CAR) phenological survey: leaf loss (yellow), flowering (pink), or fruiting (red) is shown for each species. The number (n) of trees monitored over the 2007-2018 period is also indicated. Unpublished results.

We will also examine the between- and within-site variations in deciduousness and test for the proximal and ultimate control on phenology. In southern African woodlands, a pre-rain greenness was identified from information derived from regular photographs in the field and remote-sensing observations (Ryan *et al.* 2017), arguing for an ultimate rather than a proximal control. In central Africa, contrasted seasonality is also expected between northern (M'Baïki) and southern (Lopé, Luki) sites (Ouédraogo *et al.* 2020) due to a six-month delay in the dry season on both sides of the Equator (van Schaik *et al.* 1993). In the CANOPI project, we will focus on leaf phenology, *i.e.*, leafing and leaf loss, using **daily photographs made by PhenoCams** installed in the field. A total of 11 PhenoCams have been installed in Lopé NP in Gabon (Figure 28) and one PhenoCam is also running in Luki, DRC. In the CANOPI project we aim to have 10-15 PhenoCams in the key sites (Lopé and Luki, and possibly Yangambi) and for a set of 5-10 canopy trees per PhenoCam, including evergreen and deciduous species, the analysis of canopy greenness throughout the year will be associated with seasonal variation in stem growth captured with dendrometers similarly to our pioneering work on *Prioria balsamifera* in Luki, DRC (Angoboy Ilondea *et al.* 2021). There is an important buffering effect of internally stored water in permanent plant structures (Borchert 1994) that might prevent leaf loss for some species. It is

64

therefore crucial to better understand phenological patterns of many species, in relation to stem water status, which can be derived from dendrometer readings (Zweifel *et al.* 2016).

Here, I present the first results of the PhenoCam network installed in the forest-savanna mosaic of Lopé NP, Gabon, and the **analytical framework developed for image processing** by Lena Royen during her master's internship. Among the set of PhenoCams running at Lopé (Figure 28), three PhenoCams pointing on forest patches and with c. two years of monitoring were selected (PhenoCams 005, 006 and 007). These PhenoCams were installed in September 2019 and were parametrized to collect each day two JPEG images (6080 × 3420 resolution, ~ 3 Mo), one at 11 am and one at noon to limit the influence of the sun angle (Alberton *et al.* 2017).
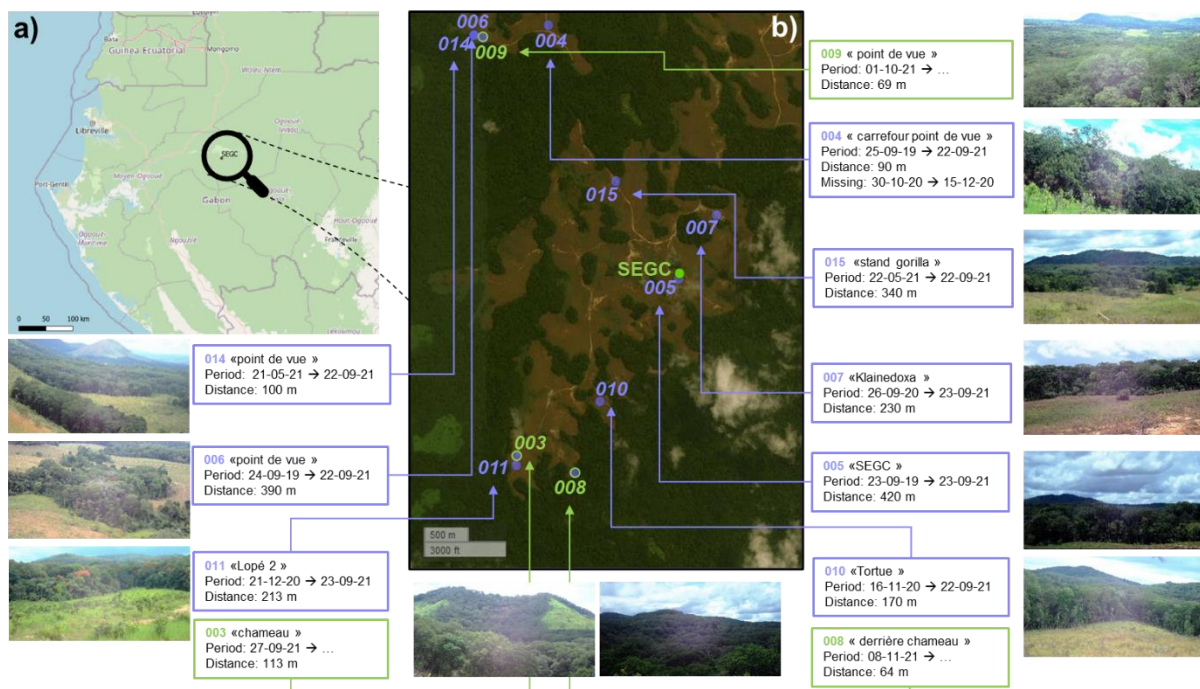

Figure 28. PhenoCam network installed in Lopé NP, Gabon. Location of the research station for gorillas and chimps in Gabon (SEGC, a) and network of PhenoCams installed in the field (b). The monitoring period and distance to forest is given for all PhenoCams so as a view of the reference scene. Colors distinguish the PhenoCams installed in 2019 and 2020 from that installed in 2021 (green). The background maps were extracted from the mapview library in R and correspond to OpenStreetMap (a) and land cover from Esri.WorldImagery (b).

From the 24th of September 2019 to the 22nd of September 2021, the PhenoCams 005, 006 and 007 gathered respectively 1,465, 1,181, and 1,459 raw images (Figure 29), the number of images is different because of technical problems in image acquisition due to wind or maintenance. Each JPEG image consists of three layers, one for each primary Red Green Blue (RGB) color, and each pixel contains a digital number corresponding to the intensity of each primary color. The first step in the processing of these PhenoCam images is to select a

reference image that fixes the field of view for each PhenoCam (step 1 in Figure 29). These images can be used to study the seasonal functioning of the canopy, as a whole, or for some Specific Regions Of Interest (ROIs) corresponding to specific crowns (Alberton *et al.* 2017), ROIs are manually digitalized in QGIS and here included the extent of the forest and savanna, separately, and the crown of individual trees that were identified to species in the field. The ROI shapefiles are then transformed into raster masks in the R open environment (R Development Core Team 2018), but the *phenopix* R package also offer a ROI digitalization directly in R (Filippa *et al.* 2016) which however seems less precise than what was done here in QGIS.
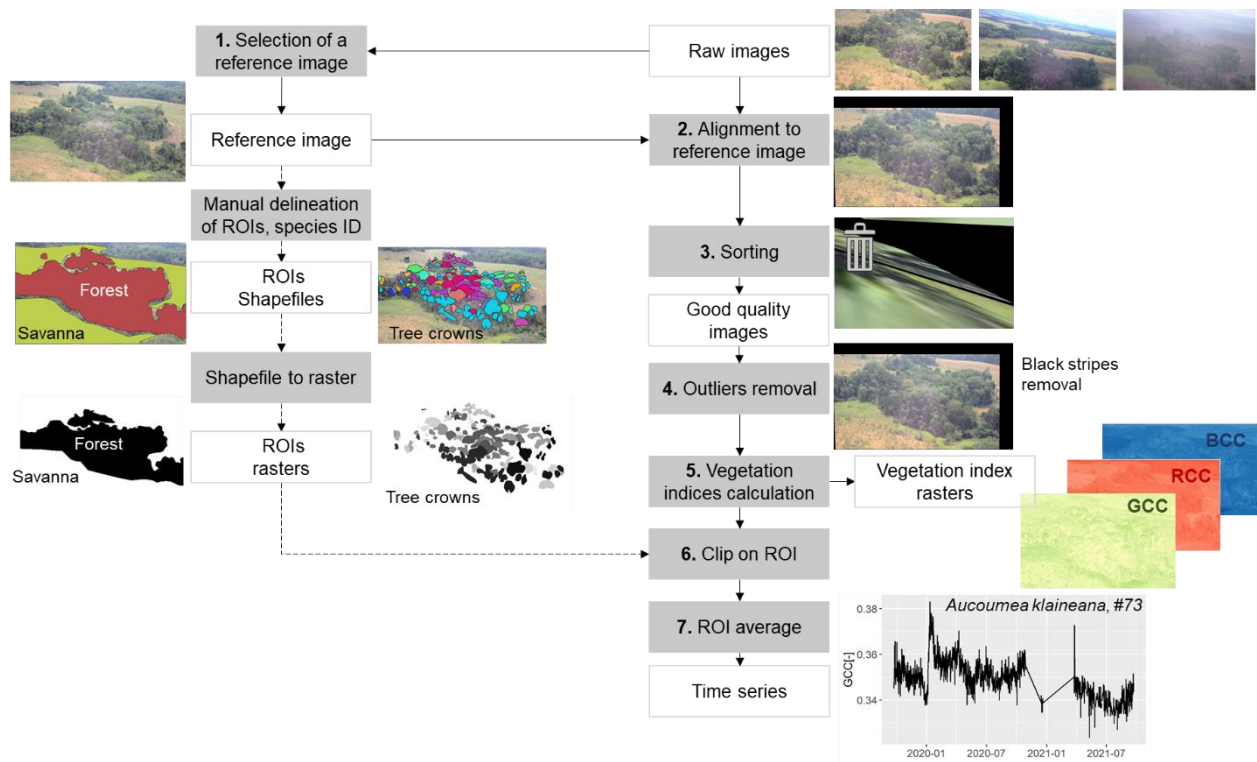

Figure 29. Analytical framework developed for the processing of PhenoCam images. The first step corresponds to the selection of a reference image used to delineate the Regions Of Interest (ROI). In a second step, all images are aligned on the reference image. Aligned images are then manually sorted in a third step and black stripes due to changes in the view are removed in a fourth step. Vegetation indices are then calculated at the pixel level (step 5) and clipped and averaged over the ROI (steps 6 and 7).

Fluctuations in the angle of view occurred due to the wind or the PhenoCam handling during maintenance (every three months, for verifying the battery level and the accurate image acquisition). It was thus needed to align all images on the reference image (step 2 in the framework, Figure 29) and this was carried out via A-KAZE and ECC methods running with a python code earlier developed (Dandrifosse *et al.* 2021). The principle is that all images in the time series (called "slaves") are individually geometrically transformed so that the objects coincide with the same objects in the reference image (called "master"). Poor-quality images due

to the bad weather (heavy rainfall, dense clouds) and/or faulty alignments on the reference image are then sorted and removed visually (step 3 in Figure 29). Then, areas not common to the reference image and represented by black stripes are removed from the image based on RGB thresholding, with black corresponding to zero values for R, G, and B (step 4 in Figure 29). Vegetation indices can then be computed for each pixel in each image, but for now we only worked with the Green Chromatic Coordinate (GCC) which translates the intensity of green (step 5 in Figure 29).

$$GCC = G / (R + G + B) \hspace{4cm} \text{(eq. 4)}$$

The GCC is part of the RGB 'chromatic coordinates' indices early developed for remote-sensing and is recognized as the most effective vegetation index for extracting leaf color changes independently of light variation between RGB images (Gillespie *et al.* 1987; Sonnentag *et al.* 2012; Alberton *et al.* 2014). Depending on the degree of green, the GCC will be sensitive to the leaf loss but also to leaf maturity whose color varies with age as shown for the Caatinga in Brazil (Roberts *et al.* 1998). This index has been used to detect leafing in the Amazon (Lopes *et al.* 2016) and in Borneo (Nagai *et al.* 2016), and to monitor greening in the Cerrado (savanna) vegetation of Brazil (Alberton *et al.* 2014) and other seasonally dry communities (Alberton *et al.* 2019). Afterwards, the GCC pixel values were clipped and aggregated (steps 6 and 7 in Figure 29) for each image over the ROIs at the scale of the community (forest *versus* savanna) and of tree crowns for forest trees.

In this preliminary work, the GCC was first averaged for the ROIs corresponding to the forest and to the savanna (in green and yellow, respectively in Figure 30). The GCC varied between 0.28 and 0.40 over the two years but unfortunately, due to technical problems, the time series are not complete since the PhenoCams did not take any images during one (PhenoCams 005 and 007) and two (PhenoCam 006) time periods. There is a lot of noise in the GCC raw data as shown by the large variation between daily observations and consecutive days. I first handled this problem with the fit of GAMM models depicting the major trends in the time series. For the forest ROIs, the variation throughout the year appears bimodal, with two peaks during the rainy seasons observed in the GCC raw data and in the GAMM predictions, and two hollows during the dry seasons (in grey, Figure 30), the hollows being larger at the end of the long dry season (JJAS). This bimodal trend in forest greenness is less clear for the PhenoCam 005 probably because the peak in greenness was a bit earlier than the start of monitoring, end of September 2019, and also, because the data recorded by this particular PhenoCam 005 oriented toward the edge of the forest rather than over the canopy are noisier with large daily and weekly variations (Figure 30a). For the two other PhenoCams, 006 and 007, the range in GCC values observed

for the forest ROI is much more restricted, between 0.34 and 0.35, as observed in dry tropical communities in Brazil (Alberton *et al.* 2019). For the savanna ROIs, the seasonal variation shows a broad peak at the end of the rainy season (ON) that can last till the short dry season (DJF, in grey in Figure 30) during which the GCC starts decreasing up to the strong hollow observed in September at the end of the long dry season when the savanna is burnt (lowest GCC value). Shortly after burning, savanna GCC values sharply increase and follows the same cycle, with a maximum at the end of the rainy season possibly extending to the short dry season before the progressive decline up to the end of the long dry season (JJAS). The range of GCC values are larger in the savanna ROIs than in the forest ROIs for the same PhenoCam, and GCC ranges tend to be greater for the PhenoCam 007 oriented toward the edge (Figure 30c) rather than for the PhenoCam 006 with a view over the forest-savanna mosaic (Figure 30b).
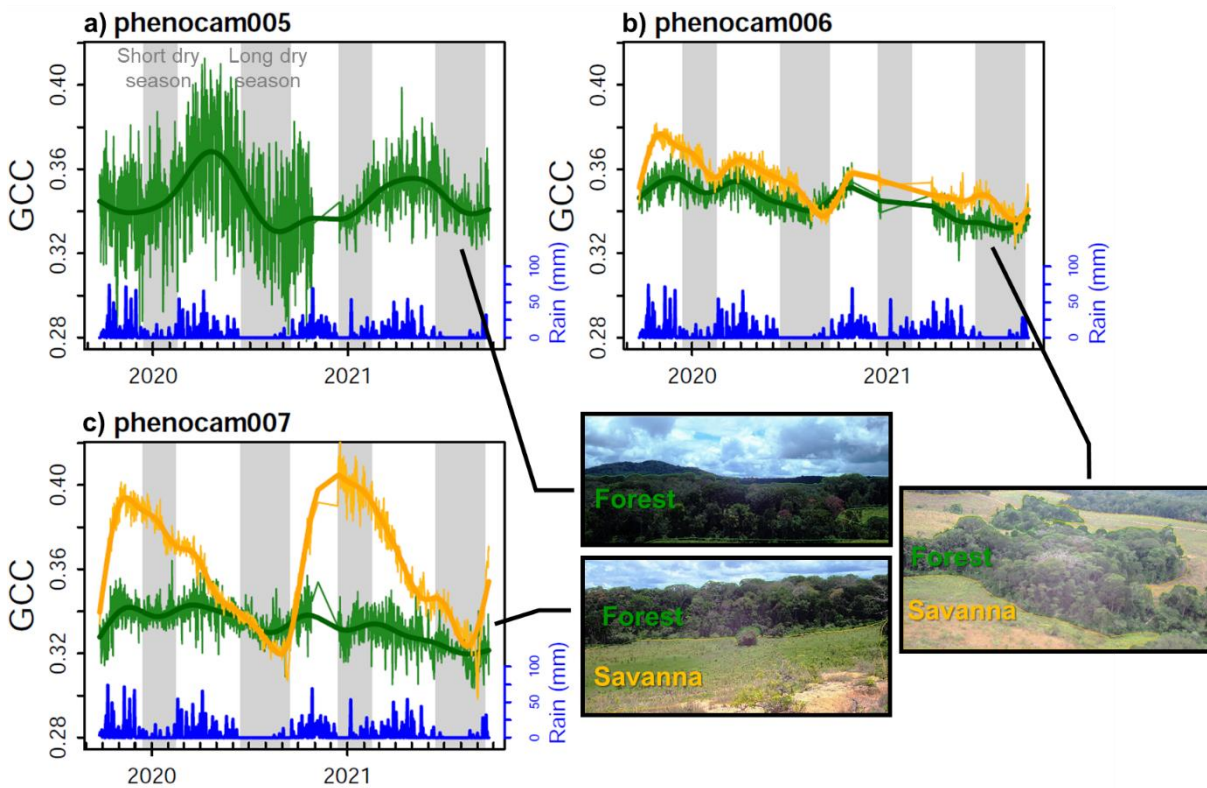

Figure 30. Seasonal variation of greenness in forest and savanna of Lopé NP in Gabon. The variation of the Green Chromatic Coordinates (GCC, dimensionless) is shown for the three PhenoCams, 005 (a), 006 (b) and 007 (c), installed in Lopé NP and for which a two-year time series is available. The corresponding reference images are shown as inset. The lines correspond to the predictions of a GAMM model fitted separately for the forest (green) and for the savanna (yellow) on the ROI average for each image. Dry seasons recognized in the area are shown in grey starting with the short dry season (DJF) and the long dry season (JJAS). Daily rainfall (in mm) measured onsite is shown in blue. Unpublished results.

Then, I started analyzing the phenology information at the scale of individual crowns for the PhenoCam 006 which offer an accurate view on the canopy. Due to missing data, I only

analyzed the first-year time series (from the end of September 2019 to the first of October 2020). I also reduced the noise in the GCC data by keeping the 90th percentile of observations over three consecutive days as earlier proposed by Sonnentag *et al.* (2012). I then fitted GAMMs to these filtered GCC time series separately for each individual crown using the restricted maximum likelihood smoothing method and the number of basic functions was set to 20. To determine the phenological phases, I followed the approach established by Lopes *et al.* (2016) for trees in the Amazon basin but I adapted the thresholds according to the crown observations on the images. Specifically, I identified (i) leaf loss or deciduous crowns as crowns with a low GCC (< 20th percentile) and an abrupt drop in GCC values (monthly decrease in GCC lower than minus the half the yearly range) and (ii) crowns with a leaf flush as crowns with a high GCC (> 80th percentile) and an abrupt increase in GCC (monthly increase in GCC greater than half of the yearly range). I then analyzed the duration and number of these phenological events at the species level.
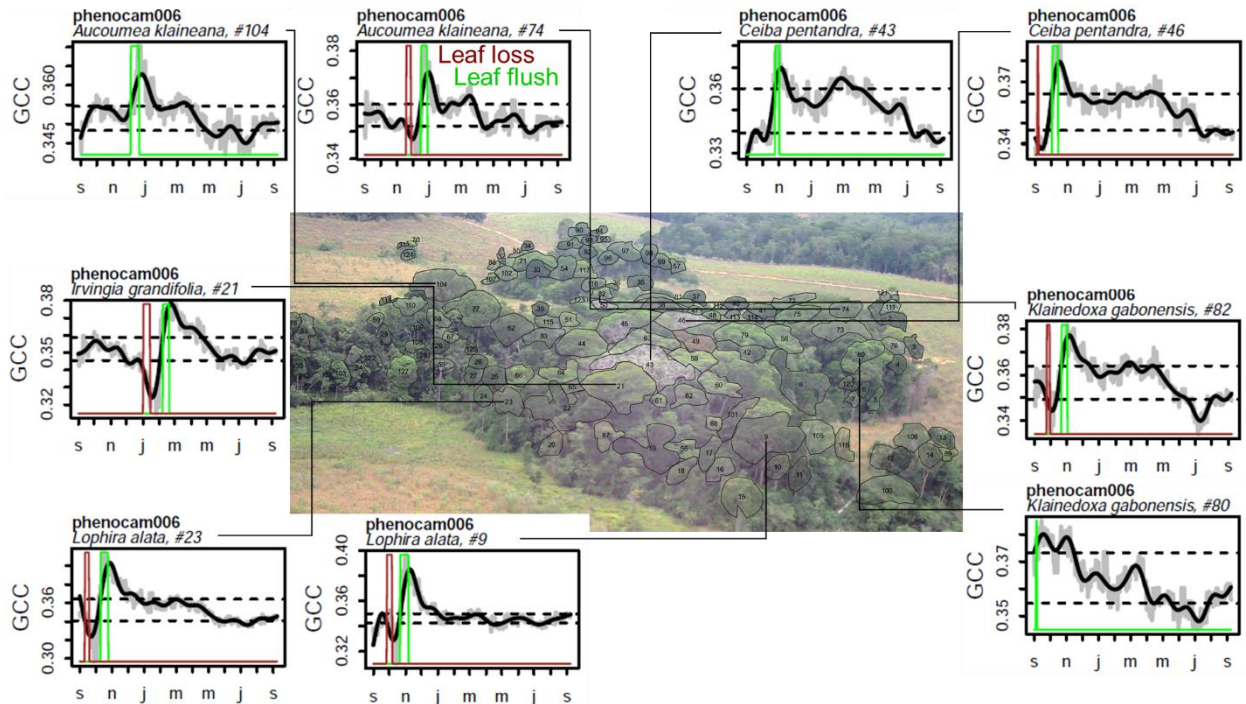

Figure 31. Leaf loss and leaf flush detection from PhenoCams. Variation of the Green Chromatic Coordinates (GCC, dimensionless) is shown for nine individual crowns belonging to five species and visible on the PhenoCam 006 installed in Lopé NP. GCC seasonal profile over a single year, from September 2019 to September 2020 are related to the crown location on the reference image shown as background. A GAMM model (black) was fitted on the GCC data (in grey) that were previously filtered (90 percentile over three days of observation). The phenological events detected are also shown on the GCC seasonal profile, with leaf loss (in brown)/flush (in green) identified as a low/high GCC following an abrupt decline/increase. The dashed lines represent the percentile 20 and 80 used to determine a low/high GCC value for each GCC time-series. Unpublished results.

Depending on the tree phenology, I was able to detect both leaf loss and leaf flush for the same crown, such as for the *Aucoumea klaineana* #74, the *Irvingia grandifolia* #21, the *Lophira alata* #23 and #9, the *Ceiba pentandra* #46, and the *Klainedoxa gabonensis* #82, though overall I detected more leaf flush (n=138) than leaf loss (n=57) events. This lower number of leaf loss events can be explained by the presence of evergreen trees/species that never shade their leaves totally, though they show intense greening events (considered here as leaf flush), and also by the fact that some trees were already deciduous at the start of the monitoring (end of the long dry season), and our approach fails to detect the abrupt decrease such as for the *Ceiba pentandra* #43 which is clearly deciduous on the reference image (Figure 31). In addition, I detected several leaf flush events for some trees and species, while some trees and species appeared relatively regular such as *Lophira alata* (see the reddish crowns on the title page and on the video, https://www.youtube.com/watch?v=HXbe0ppq30s). These events are relatively short in time, barely longer than 10 days, and thus not detectable with other approaches.

To conclude on this preliminary work, the two years of images taken by the three PhenoCams show that forest canopy seasonal functioning is bimodal, mimicking rainfall seasonality, the two peaks in the vegetation index corresponding to the two rainy seasons, while savanna functioning is unimodal, with a minimum during the long dry season (Figure 30). The analysis of individual crowns for forest trees identified in the field and manually digitalized on a reference image, highlighted that leaf loss and leaf flush are extremely brief phenomena (< 10 days for most species). This work is encouraging and will be improved and extended in the frame of the CANOPI project. Other vegetation index and approaches (deep learning) will notably be explored. However, the challenge is to improve the quality of image acquisition in the field and to maintain PhenoCams over the long-term. Two PhenoCams were recently damaged by lightning and several PhenoCams ceased functioning without any apparent reason. Also, it is important to maintain field observations for reproductive phenology, which have been demonstrated to be impacted by climate changes recorded on-site (Bush *et al.* 2020a) and the long-term collapse in fruit ability threatens the megafauna (Bush *et al.* 2020b).

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