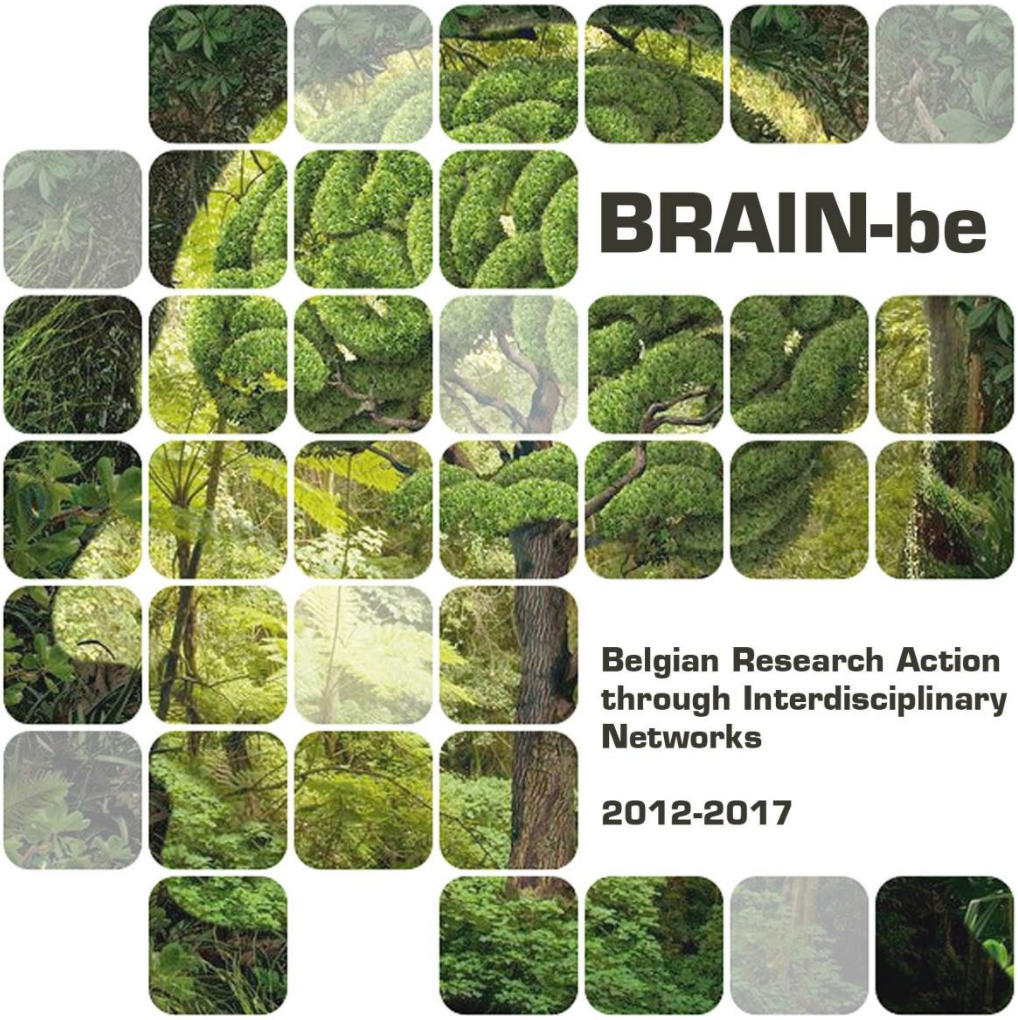

AFRIFORD

Genetic and paleoecological signatures of African rainforest dynamics: pre-adapted to change?

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AFRIFORD

Genetic and paleoecological signatures of African rainforest dynamics: pre-adapted to change?

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1. INTRODUCTION

Tropical forests are continuously at the centre of international debates on the carrying capacity of the planet, mainly because of the growing pressure on their carbon stocks, their threatened species richness and the manifold ecosystem services they provide. According to Pan et al. (2011), current land-use changes in the tropics represent an annual carbon source of approximately 1.3 Pg C. These land-use changes are also the principal threat for biodiversity. Forest fragmentation and overexploitation lead to a decline in tree diversity and of their commensal wildlife populations, ultimately leading to the disappearance of some ecosystems services on which both local and distant human populations depend. Because the estimates for the tropics still have large uncertainties, there is a dire need for studies on rainforest dynamics both in terms of carbon fluxes and biodiversity changes. A review by Gibson et al. (2011) showed that most forms of forest degradation have an overwhelmingly detrimental effect on tropical biodiversity, but only few studies were conducted in Africa.

2. STATE OF THE ART AND OBJECTIVES

Long-term stability against environmental change has been considered for long as a prime cause of the remarkable biodiversity of tropical rainforests. However, paleoecological evidence of substantial change in the vegetation of tropical regions resulting from global climate fluctuation during the Quaternary, as well as evidence of significant ecological perturbation by humans in the last few thousand years, call for a reassessment of the temporal dynamics of biodiversity in tropical rainforests, and how this may influence their resilience and/or adaptation to rapidly accelerating human impact. The evolutionary and environmental history of the Central African rainforest, in particular, is barely known while its remarkable biodiversity is threatened.

Therefore, the **general objective** of AFRIFORD is to **understand how past climate changes and the activities of ancient indigenous societies have shaped the current distribution and composition of African rainforests and the genetic diversity of their constituent tree species**. This knowledge is essential for forecasting how the forest will respond to current and future environmental impacts, because the way tropical forests have responded to past climatic and human perturbation reveals their resilience, or innate adaptive capacity, to current and future perturbations resulting from massive ongoing deforestation, forest degradation and anthropogenic climate change.

The **specific scientific objectives** of AFRIFORD are to:

1) **Understand the processes leading to the diversification/differentiation of African rainforest tree biodiversity** at inter-specific and intra-specific levels, in particular the respective roles of (i) past population fragmentation and the associated genetic drift (neutral stochastic process) and (ii) differential selection leading to adaptation to different habitats along environmental gradients (deterministic process).

2) **Document the main climatic and anthropogenic perturbations which affected the past vegetation dynamics in the Congo basin** for a range of relevant time scales, with particular emphasis on (i) the last glacial-interglacial cycle, (ii) the late Holocene where traces of forest fire become abundant, and (iii) the last two centuries when current tree communities were established.

3) **Develop and calibrate a vegetation model** able to simulate reliably the changes in (i) vegetation, (ii) productivity, and (iii) species distribution ranges in response to environmental forcing, in order to make predictions under scenarios of climate and anthropogenic environmental changes.

These objectives were achieved through multi-disciplinary research integrating paleoecological analyses (palynology, anthracology) on lake and soil sediments, dendrochronology, vegetation modelling and population genetics.

This project has great societal relevance for local populations, regional governments and the international community by its generation of key new knowledge on the sustainability and resilience of African rainforest biodiversity and the diverse ecosystem services it provides. Project results support Belgian government policy in the context of the international programmes CITES, FLEGT, MAB and REDD+, among others, by transforming this knowledge into projective tools for sustainable management of African rainforest.

Within BRAIN.be thematic axes, AFRIFORD is relevant to the theme 'UNDERSTANDING BIODIVERSITY AND EVOLUTION OF ECOSYSTEMS' through its integration of multi-disciplinary fundamental research aimed at developing the conceptual, methodological and factual basis for understanding the general processes controlling the dynamics of biodiversity in African rainforest. AFRIFORD is also relevant to theme 'PRESSURES ON BIODIVERSITY AND ECOSYSTEMS, AND IMPACTS', by assessing the adaptive potential of tree species and resilience of tree communities with respect to climate change and anthopogenic pressures in the Congo basin forest.

AFRIFORD provides fundamental scientific insights relevant to define policies for the sustainable management of biodiversity and ecosystems:

i. Key knowledge on the biodiversity of the African rainforest from the intraspecific to the community level, and its capacity to resist/adapt to on-going environmental changes.

ii. Highly qualified training on African rainforest biodiversity and ecosystem functioning for both European and African students involved in the project.

iii. Translation of scientific knowldegde to key actors of the society (institutions, NGO's, forestry companies,...) through conferences and the diffusion of documents.

For policy support, AFRIFORD provides fundamental scientific knowledge in support of:

- CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora): the use of genetic markers (i) allows to re-assess species delimitation and hence tree species richness, a central concept for conservation biology; (ii) allows to assess the organisation of the genetic diversity of timber species which is an important component to evaluate the risks associated with their exploitation (e.g., *Pericopsis elata*, one of the CITES-protected African tree).

- FLEGT (Forest Law Enforcement, Governance and Trade, the European Union Action Plan against illegal logging, seeking to exclude illegal timber from its markets): phylogeographic data help identify the geographic origin of traded wood.

- MAB (Man and the Biosphere, UNESCO Programme to promote interdisciplinary approaches to management, research and education in ecosystem conservation and sustainable use): two of the focal study sites in the Democratic Republic of Congo, Yangambi and Luki, belong to the network of MAB Biosphere Reserves, so that the scientific work benefits from the UNESCO-MAB programme for its diffusion.

- REDD+ (Reducing Emissions from Deforestation and Forest Degradation "plus" conservation, seeking the sustainable management of forests and enhancement of forest carbon stocks): the vegetation model developed helps predict carbon emission and stocks following vegetation changes.

At the national level, AFRIFORD is also complementary to the BELSPO-funded projects BIOSERF, CLANIMAE, COMBINFO and HERBAXYLAREDD.

3. METHODOLOGY

The implementation of the AFRIFORD project is structured around eight workpackages (WP) that are complementary in terms of system integration and time scales (Fig. 1).

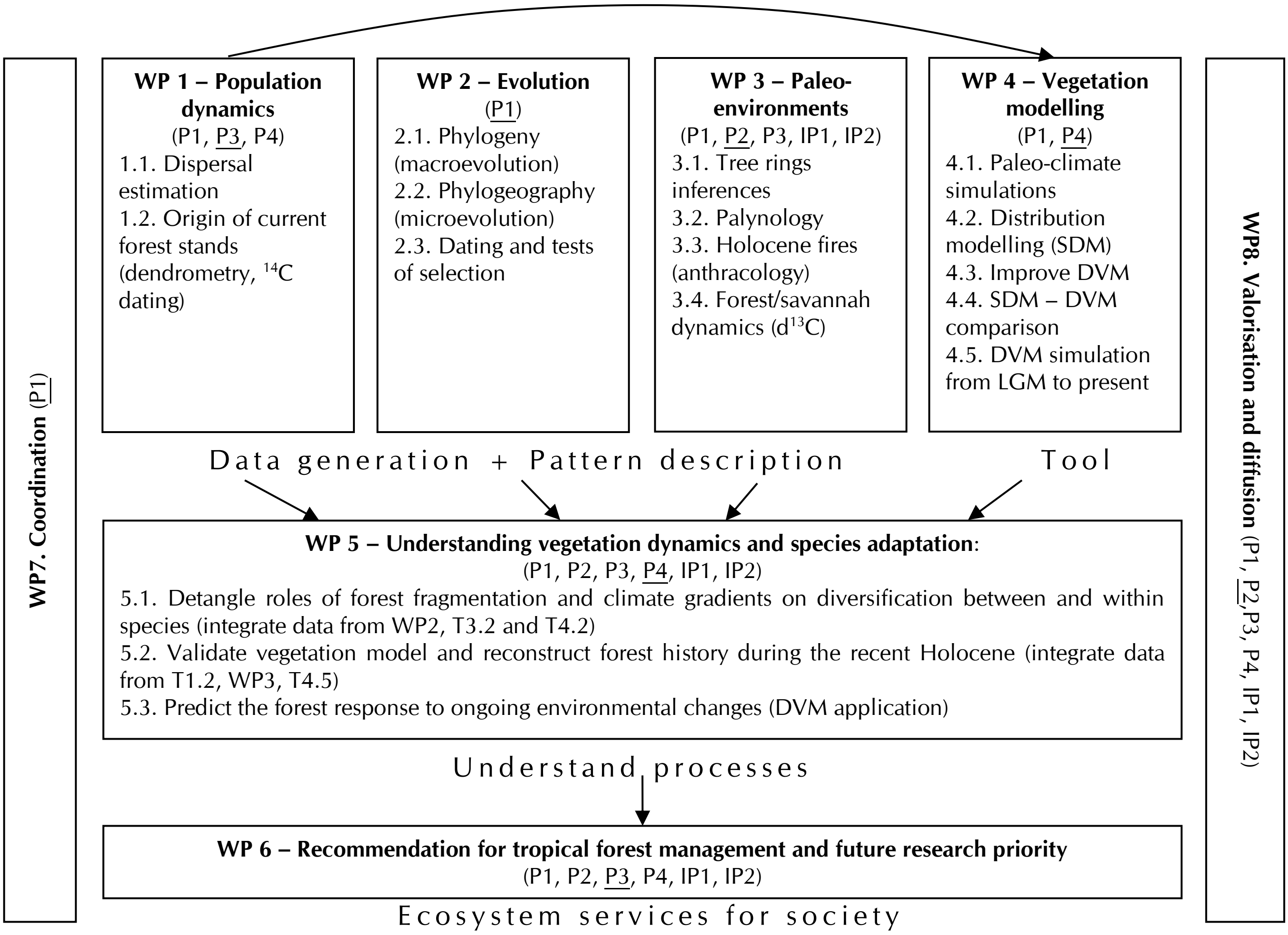


Figure 1. Chart of workpackages. WP1 to WP3 focus on the generation of new data and description of biodiversity patterns in space and time, to document the dynamics of tree populations, the evolution of tree species, and the history of vegetation changes recorded in natural archives. WP4 focuses on vegetation modelling (processes simulation) and provides a tool to forecast the response of regional vegetation to future climate change. WP5 is multi-disciplinary, and integrates the information provided by WP1-4 to understand the processes determining vegetation dynamics and tree species adaptation to change in the context of the wider African rainforest ecosystem. At the end of the project, WP6 extracts from the acquired scientific knowledge the conclusions relevant for policy making in biodiversity conservation and forest management. WP7 and WP8 are transversal workpackages dedicated to the coordination of the project activities, and the valorisation and diffusion of the project outputs, respectively. Involved Belgian partners (P's) and international ones (IP's) are indicated, coordination within each WP being under the responsibility of one partner (underlined). P1 = ULB, P2 = UGent, P3 = RMCA, P4 = ULg, IP5 = LOCEAN, IP6 = UBern.

Outline of the methodology:

WP 1 – Population dynamics

This WP aimed to gather information on the current dynamics of tree populations in the Congo Basin, focussing on (1.1) the scale of seed and pollen dispersal, and (1.2) the origin of current forest stands, in order to better understand how fast species can disperse in a landscape and what is the typical timescale of the sylvogenetic cycle.

1.1. Estimation of tree dispersal, using genetic tools.
We used genetic markers to identify the parents of seeds and seedlings in exhaustively inventoried plots (direct method) or to describe the spatial genetic structures for different tree species (indirect method), allowing to estimate the range of seed and pollen dispersal distances (Ley & Hardy 2016; Ewédjè et al. 2017; Hardy et al. 2019).

1.2. Origin of current forest stands.
We used tree rings as well as ring dating and tree diameter growth to estimate the age of trees as well as the age of forest stands which can reveal when perturbations occurred in the case of pioneer light-demanding species (Hubau et al. 2019).

WP 2 – Evolution

This WP aimed to exploit genetic signatures informing on (2.1) the patterns of tree evolution to better understand the factors driving speciation, and hence the remarkable biodiversity of tropical forests, (2.2) the patterns of genetic diversity within species to identify potential cryptic species (hidden species diversity) and better understand how past climatic events affected the genetic diversity, and (2.3) the timing of speciation and population differentiation events, to assess the timescales at which evolutionary processes occur.

2.1. Macro-evolution: a comprehensive phylogeny of African rainforest trees.
Plastid gene sequences (produced by the project and extract from GenBank database) were used to construct a large phylogeny of African plant species for all angiosperms (Janssens et al. 2020), which is appropriate to reveal links between genera. Plastid or nuclear sequences were used to decipher the evolution within several tree genera (Donkpegan et al. 2017; Tosso et al. 2018; Monthe et al. 2019).

2.2. Micro-evolution: phylogeography of African rainforest tree species.
Microsatellite genetic markers were used to characterize the genetic structure of different tree genera, allowing to (i) identify cryptic species (Ikabanga et al. 2017; Monthe et al. 2018; Lissambou et al. 2018, 2019), (ii) identify signatures of past population fragmentation (Demenou et al. 2016, 2018, 2020; Donkpegan et al. 2020a, 2020b; Ley et al. 2017; Migliore et al. 2019, 2020; Piñeiro et al. 2017; Vanden Abeele et al. 2019).

2.3. Dating.
DNA sequences and fossil calibration points were used to estimate the divergence time between species or between populations of the same species, providing a timescale at which evolutionary processes happens (Demenou et al. 2020; Migliore et al. 2019, 2020), allowing to confront them to recorded paleaoenvironmental events (see next WP).

WP 3 – Paleo-environments

This WP aimed to exploit different paleo-environmental signatures informing on (3.1) recent climate changes recorded in tree rings, (3.2) the history of vegetation and fires during the Holocene and recent Pleistocene as recorded from pollen and micro-charcoal found in lake sediments, (3.3) the Holocene fires recorded in macro-charcoal from forest soil, (3.4) the forest/savannah dynamics during the Holocene recorded from soil profiles of $\delta^{13}C$.

3.1. Document climate changes of past 200 yrs from tree ring isotopes
Climatic proxies were tentatively extracted from C and O isotopes detected in the annual tree rings of *Pericopis elata* (Colombaroli et al. 2016).

3.2. High-resolution reconstruction of past forest dynamics: palynology and fossil charcoal from lake-sediment cores.
The vegetation and fire histories around lakes from near the western (Cameroon) and eastern (Uganda) periphery of the African rainforest were reconstructed at high temporal resolution using pollen and macroscopic (>150 μm) charcoal preserved in sediments (Lézine et al. 2019; Nolan et al. 2018; Verlhac et al. 2018).

3.3. Document Holocene fires.
Soil charcoal from different sites of the Congo basin were studied through analyses of stratigraphic distribution, ^{14}C dating and botanical identification to assess where and when fires occurred and whether the forest community changed of botanical composition after fire events (Hubau et al., in prep.).

3.4. Reconstruct forest/savannah dynamics from δ^{13}C of soil samples.
The relative abundances of plants performing photosynthesis following a C4 (dominant in savannas) or C3 (dominant in forest) metabolism affect the isotopic composition of soil carbon, leaving an evolving δ^{13}C depth profile after a forest/savannah vegetation change. This property was exploited to reconstruct past forest/savannah vegetation change in different sites in Cameroon close the forest/savannah limit (Desjardins et al. 2020).

WP 4 – Vegetation modelling

This WP aimed to use the Dynamic Vegetation Model (DVM) CARAIB, as well as niche-based modelling (SDM), to attempt to reconstruct or project species/vegetation distributions in the past or in the future.

4.1. Acquisition of paleo-climate simulations, tests and downscaling to the Guineo-Congolian region
Regional climate modelling was performed over Equatorial Africa at a 50-km spatial resolution with the regional climate model MAR (Gallée et al., 2004), first to simulate present climate (1970-1999) and then to produce palaeoclimatic reconstructions since the Last Glacial Maximum (LGM, 21 ka). Unfortunately, for the present, Doutreloup et al. (2017) showed that the MAR model forced with NCEP1 reanalyses (chosen for their available 6-hourly outputs, required to run the MAR) failed to reproduce tropical climate. It better reproduced the quantities as well as the annual rainfall regime in the semi-arid regions than in equatorial regions. In equatorial regions, the comparisons of temperature and precipitation with NCEP1 reanalysis highlighted an underestimation of precipitation amount by the model, leading in turn to too high surface temperature. The main reason was an inadequate convective scheme for reproducing tropical climate and possibly a bad representation of vegetation (rainforest type) in the model. Therefore we have not exploited the MAR outputs directly and rather used the GSWP3 (20 CR) time series as present climate (1971-2000). This dataset is derived from reanalyses statistically downscaled at a 0.5°x0.5° resolution and bias-corrected with respect to available observation data. It was prepared and distributed in the framework of the Inter-Sectoral Impact Model Intercomparison Project Phase 2a (ISI-MIP2a), in which CARAIB participated.
For the palaeoclimatic conditions, to avoid MAR biases, we used the GSWP3 (20 CR) time series as present climate (1971-2000) and we added to this reference the climatic anomalies between LGM/Mid-Holocene and present period calculated by the regional climate model. MAR was nested in the outputs of the CNRM-CM5, FGOALS-g2 and MRI-CGCM5 global climate simulations from the PaleoModelling Intercomparison Project (PMIP3, https://pmip3.lsce.ipsl.fr/) for the mid-Holocene (6 ka) and LGM snapshots. Mid-Holocene colder temperature and wetter conditions are best reproduced by the MAR nested in MRI-CGCM5. This MAR-MRI combination also simulates well the

important reductions in temperature and in precipitation during the LGM. Therefore, we only focused on this experiment in the following results.

4.2. Distribution and niche modelling of selected species

As a tool to ascertain current distribution, multiple logistic regression was applied. This method has the best theoretical background and performs as well as other methodologies used for niche modelling. Each set of species occurrences was balanced with a set of pseudo-absences randomly drowned in a buffer of 2,000 km around the occurrences and the best set of explaining climate factors (linear and pairwise effects) was selected on the basis of the AIC following exhaustive search.

4.3. Improvement of CARAIB model

Originally dedicated to simulate the vegetation globally, dynamic (global) vegetation models use vegetation classifications to represent the largest set of plant species. CARAIB uses extended classification including 26 Plant Functional Types: 3 herbaceous, 8 shrubby and 15 arboreal PFTs. Two PFTs represent tropical humid forest: the broadleaved evergreen and raingreen tropical trees. As illustrated in "Main project results - 5" below, the vegetation model is also used to simulate distribution of tropical African vegetation at the species level to better project and understand past or future dynamics. For the project, we determined climatic requirements and gathered some specific traits for 91 species:

- *Set of 91 tree species*
- *Evergreen and deciduous species including mountainous taxa*
- *Climatic requirements determined from present distribution (RAINBIO database)*
- *Simulated with C3 and C4 grasses and few shrubs*

1 Afrocarpus
2 Afzelia
3 Afzelia africana
4 Afzelia_bella
5 Afzelia_bipindensis
6 Afzelia_pachyloba
7 Afzelia_quanzensis
8 Alstonia boonei
9 Amphimas pterocarpoides
10 Annickia chlorantha
11 Anonidium mannii
12 Anthonotha_macrophylla
13 Antiaris toxicaria
14 Baillonella_toxisperma
15 Blighia welwitschii
16 Carapa procera
17 Ceiba pentandra
18 Celtis africana
19 Celtis tessmannii
20 Celtis zenkeri
21 Cleistopholis glauca
22 Coelocaryon preussii
23 Cola acuminata
24 Cynometra hankei
25 Dacryodes edulis
26 Dialium pachyphyllum
27 Distemonanthus_benthamianus
28 Elaeis guineensis
29 Erythrophleum_ivorense
30 Erythrophleum_suaveolens
31 Fillaeopsis discophora
32 Ganophyllum giganteum
33 Garcinia epunctata
34 Garcinia kola
35 Garcinia punctata
36 Greenwayodendron suaveolens
37 Guarea cedrata
38 Guibourtia demeusei
39 Hagenia abyssinica
40 Harungana madagascariensis
41 Hymenocardia ulmoides
42 Ilex mitis
43 Irvingia gabonensis
44 Juniperus procera
45 Lannea welwitschii
46 Lophira alata
47 Lophira lanceolata
48 Macaranga monandra
49 Macaranga spinosa
50 Maesopsis eminii
51 Mammea africana
52 Maranthes glabra
53 Milicia excelsa
54 Milicia regia
55 Millettia laurentii
56 Musanga cecropioides
57 Nauclea diderrichii
58 Olea Capensis
59 Ongokea gore
60 Oubanguia africana
61 Pancovia laurentii
62 Panda oleosa
63 Paramacrolobium coeruleum
64 Parinari excelsa
65 Pentaclethra eetveldeana
66 Pentaclethra macrophylla
67 Pericopsis elata
68 Plagiostyles africana
69 Podocarpus latifolius
70 Polyalthia suaveolens
71 Prunus africana
72 Pseudospondias microcarpa
73 Pterocarpus soyauxii
74 Pycnanthus angolensis
75 Quassia silvestris
76 Santiria_trimera
77 Scorodophloeus zenkeri
78 Staudtia kamerunensis
79 Sterculia tragacantha
80 Strombosia grandifolia
81 Strombosiopsis tetrandra
82 Symphonia globulifera
83 Synsepalum stipulatum
84 Syzygium guineense
85 Tabernaemontana crassa
86 Terminalia superba
87 Tetrapleura tetraptera
88 Treculia africana
89 Uapaca guineensis
90 Uapaca heudelotii
91 Xylopia phloiodora

4.4. SDM-DVM comparison

Forced with the same climate inputs, the species distributions simulated by the dynamic vegetation model and the SDM were compared. Both models can reproduce the current distributions. This comparison confirmed that the present realized species distributions in Africa are the result from the competition with other tree species. The DVM results not taking competition into account suggest indeed that the potential distributions may be significantly larger. This comparison also allowed a more careful analysis of the location of species glacial refugia.

4.5. Transient simulation from the LGM (21 ka) to pre-industrial times

From LGM to present time, CARAIB was also forced with the 1-ka snapshot outputs of the HadCM3 climate model (Singarayer et al., 2017), statistically downscaled at a spatial resolution of 0.5° and bias-corrected using GSWP3 (20 CR) time series.

HadCM3 anomalies display the important reductions in temperature and in precipitation during the LGM, the Younger Dryas (12 ka) still cold and dry and the mid-Holocene (7 ka) wetter conditions in Northern Africa. To simulate tree species postglacial recolonization, taking limitation by both climate and seed dispersal into account, we planned to run the dispersal module transiently on a sub-grid to reproduce species dynamics over the 21,000 years starting from their LGM refugia (simulated by CARAIB); the dispersal capacities being dependent on species productivity and survival simulated by CARAIB. As a preliminary test, the dispersal model was finally only used alone in this project without any coupling with CARAIB.

WP 5 – Understanding vegetation dynamics and species adaptation

WP5 was the multi-disciplinary integrative workpackage linking data/models from WP1 to WP4 to reveal the key processes controlling biodiversity dynamics in the Central African rainforest at short and longer time scales.

5.1. Disentangle roles of forest fragmentation and climate gradients on diversification between and within species

The objective of this task was to integrate results on evolutionary patterns (WP2), paleovegetation reconstructions (Task 3.2) and modeling (WP4). In practice, this exercise proved difficult because genetic methods captured phenomena that often appeared to have occurred (much) before the last glacial period, while paleoenvironmental methods and modelling captured time-scales spanning from the last glacial period to the Holocene.

5.2. Validate vegetation model and reconstruct forest history during the recent Holocene

Some attempts have been made to validate the modelled vegetation reconstruction for the last glacial maximum or the Holocene, with pollen data or fire history recorded in charcoals. However, the limited spatial (0.5°) and temporal (1000 years) resolution of the model snapshots combined with the very low number of data points over the African continent prevented any meaningful comparison, although some broad trends indicate an overall consistency between model and data.

5.3. Predict the forest response to ongoing environmental changes

For future climatic conditions, the outputs of 33 general circulation models (GCMs) were acquired from the Coupled Model Intercomparison Project Phase 5 (CMIP5) database of the Intergovernmental Panel on Climate Change (IPCC). We analysed the capacity of those models to reproduce the 1980-1999 annual and seasonal climate over Africa. We selected the five most performing models over present and four other GCMs producing extreme results in terms of future minimum and maximum precipitation and temperature changes in order to illustrate the range of potential climate change (see Dury et al., 2018). For each GCM, climatic anomalies between any given year and the reference 1980–1999 period were statistically downscaled to a 0.5° spatial resolution with a 2D linear interpolation and then combined to 0.5° CRU data for the reference period. We excluded the unlikely strong mitigation scenario (RCP2.6) and concentrated on more extreme scenarios of greenhouse gas forcing: RCP4.5 (538 ppmv of CO2 in 2100) and RCP8.5 (936 ppmv of CO2 in 2100), respectively representing stabilization without overshoot and rise of external forcing.

Finally, in the absence of MAR outputs of good quality, we downloaded and used some regional projections from the AFRICA-Cordex project. We chose the 0.44° (50 km) outputs of RCA4 and CCLM4-8-17 regional models, nested at the domain borders in the CNRM5-CM5 and MPI-ESM-LR global projections (chosen for their ability to simulate present-day climate and its variability, see above).

WP 6 – Recommendations for tropical forest management

WP6 focussed on the divulgation of scientific research and the recommendations during conferences and workshops.

WP7 – Project coordination

This WP devoted to project coordination concerned (i) the administration of the network and reports, (ii) the organisation of network meetings (usually twice a year for the whole network, plus occasional meetings between specific partners), (iii) the follow-up committee meetings (usually once a year, invited during one of the whole network meetings, plus specific collaborations with some members).

WP8 - Valorisation and dissemination of project outcomes

This WP focussed on the valorisation and dissemination of results.

4. SCIENTIFIC RESULTS AND RECOMMENDATIONS

Overall, the project has provided a substantial body of scientific results, already valorised in 41 peer-reviewed scientific articles (see section 6) and presented in several international conferences or workshops. Below we synthesize these outputs in 13 major themes, starting from what we learned from the long history of climate and vegetation changes as well as plant evolution, to contemporaneous problematics related to anthropogenic environmental changes. For each theme, we present recommendations for policy support whenever appropriate:

Understanding past environmental changes and their impact on biodiversity patterns:

1. Evolutionary dynamics of African trees: species show thousands to millions years old genetic signatures of past fragmentation, recolonization or demographic changes
2. Hidden species diversity and cryptic species: the African forest might contain twice more tree species than currently recognized
3. Time-correlated palynological and biomass burning signatures in lake- sediment records.
4. Vulnerability of montane ecosystems from western Central Africa: a view from the past
5. Imprint of past environmental changes in the grasslands of Cameroon
6. Charcoal analysis reveals the origin of African rainforests: seven centuries of diverging successional pathways shaped present-day compositional and functional diversity.
7. Dynamic model reconstruction of rainforest distribution change from the Last Glacial period: dispersal, an issue for species survival to climate change

Present concerns related to anthopogenic environmental changes:

8. *Pericopsis elata*, a highly exploited timber species under CITES convention that requires peculiar management due to its high level of inbreeding
9. The persistence of carbon in the African forest understory: a small tree is not always a young tree.
10. An end to the sink in intact tropical forests: a blow to global carbon sequestreation
11. The natural comeback of tropical rainforests in anthropogenic savannas: a boost to global carbon sequestration and biodiversity
12. Present realized distribution of African tropical tree species: the importance of competition between species over time
13. DVM simulations for the future show significant soil water reduction in central Africa that substantially impact the distribution and net primary productivity of the studied tree species.

Finally, we also report other outputs of the project related to the formation of African students and new collaborations.

Theme 1. – Evolutionary dynamics of African trees: species show thousands to millions years old genetic signatures of past fragmentation, recolonization or demographic changes

Most forest tree species display genetic signatures of past population fragmentation, recolonization and demographic changes dating from 10^4 to 10^6 years, highlighting long-term impacts of past environmental changes on species genetic variation.

Phylogeographic analyses were conducted on 12 tree species to (i) reveal the geographic organisation of their genetic variation, and (ii) better understand the processes driving their genetic diversity, including past climate changes. These works were published in 10 articles (Demenou et al. 2016, 2018; Donkpegan et al. 2017, 2020a, 2020b; Ley et al. 2017; Piñeiro et al. 2017; Tosso et al. 2018; Migliore et al. 2019; Monthe et al. 2019) and contributed to 4 PhD theses of African students (Donkpegan 2016; Demenou 2018; Tosso 2018; Monthe 2019). An additional study also investigated differential gene expression at the seedling stage between three *Erythrophleum* species submitted to drought stress to test if they developed different drought-resistance strategies (Neji et al. 2019).

Most of these studies are based on the use of nuclear microsatellites (highly polymorphic markers) and/or sequencing of the whole chloroplast genome and ribosomal DNA. The general emerging pattern is that most tree species are subdivided in several parapatric or allopatric genetic lineages (or genetic clusters), often coinciding with (1) Upper Guinea (West Africa), (2) the Dahomey Gap (savannah dominated corridor from Easter Ghana to Benin), (3) the north-western part of Lower Guinea (area surrounding the Cameroon Volcanic Line), (4) the north-eastern part of Lower Guinea (south-east Cameroon to the north of the Republic of Congo), (5) the southern (or southwestern) part of Lower Guinea (Gabon to southern Republic of Congo), (6) Congolia (central DRC)(Fig. 2). This confirmed the general patterns revealed by Hardy et al. (2013) and Dauby et al. (2014) for Lower Guinea, but now extended to the whole Guineo-Congolian region (i.e., West and Central African rain forests). These intra-specific genetic lineages probably originate from past population fragmentation and/or admixture events (Fig. 2), and may be past founding events after long-distance dispersal.

In tropical Africa, Pleistocene glacial-interglacial cycles, but also more recent Holocene climatic events, have often been invoked as drivers of floristic changes (e.g. Maley 1996) and the phylogeographic structure within species (Hardy et al. 2013). However, confirming these hypotheses remained difficult because the timing of population divergence has seldom been estimated for African plants before the AFRIFORD project. Our results indicate that the timescales of population divergence or admixture vary widely among species, from the early Holocene (e.g. admixture detected in the Dahomey Gap around 14 thousands years ago in *Distemonanthus benthamianus*; Demenou et al. 2016; Fig 2 upper panel) to the Pliocene or late Miocene (e.g. *Greenwayodendron suaveolens* lineages from Lower Guinea diverged 4 to 8 million years ago; Migliore et al. 2019). By contrast, late Holocene climate changes (e.g. pejoration that occurred c. 3 000 years BP) have not left detectable genetic signatures. We also observed a trend of more recent history in the case of light-demanding species and more ancient in the case of shade-tolerant species characteristic of old-growth forests (R. Piñeiro et al., unpublished). Hence, the genetic diversity of African trees built up over several millions years and, in general, phylogeographic structures cannot be explained mainly by the impact of the last glacial-interglacial cycle. Modelling species distribution during the Last Glacial Maximum

(LGM), or some other key phases of the recent Quaternary, might therefore often fail to explain contemporary genetic structures.

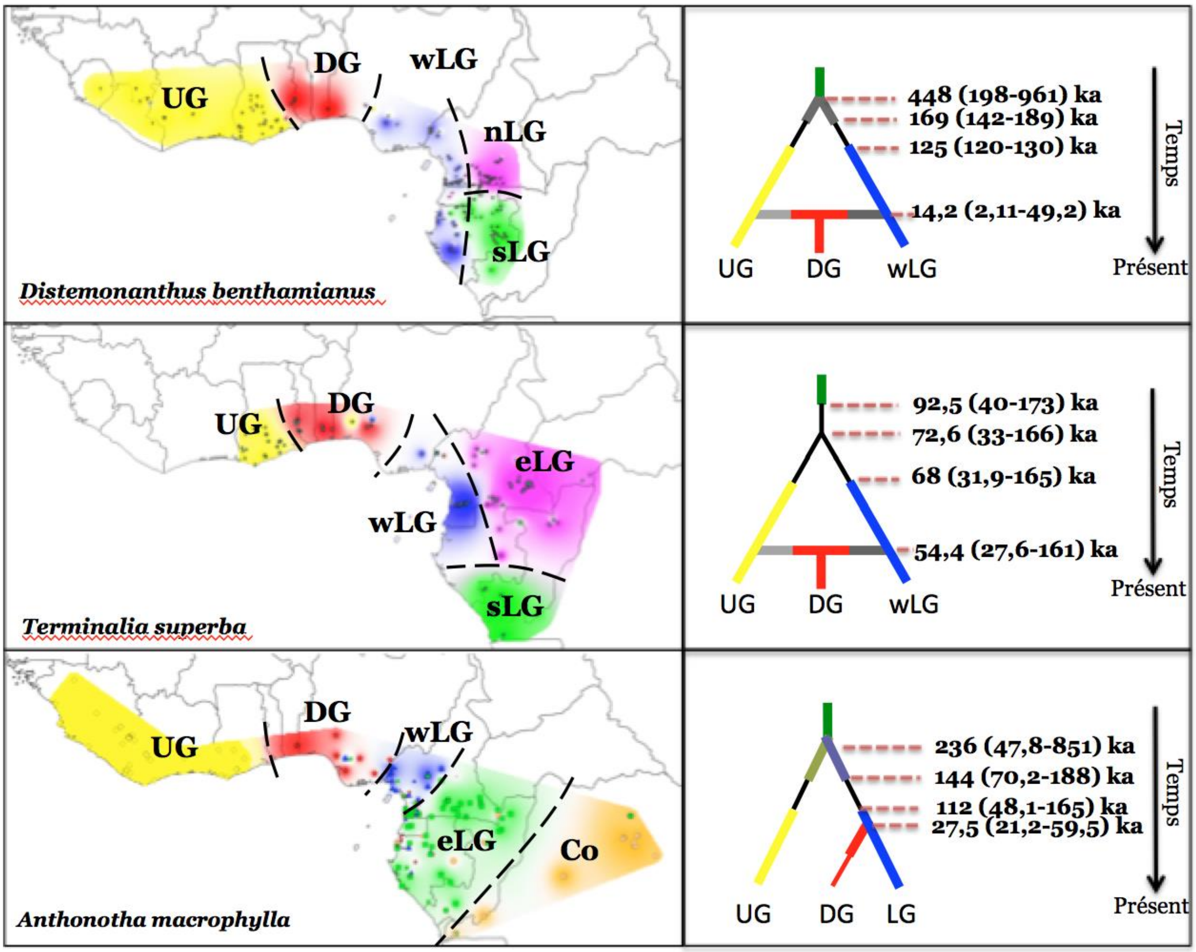


Figure 2. Phylogeographic patterns inferred from microsatellite markers in three African rainforest species (left panels, genetic clusters represented by different colors) **and timing of population divergence, mixing or demographic changes in Upper Guinea (UG), Dahomey Gap (DG) and the (north-)western part of Lower Guinea (wLG)** (right panels, time given in thousands of years before present, ka, and confidence intervals under parentheses). PhD thesis of B. Demenou (2018).

Implications for policy making

The ancient origin of phylogeographic patterns (10^4-10^6 years) implies that:

(1) tree species have been resilient to climate changes (the glacial-interglacial cycles presumably resulted in fragmentation-extension cycles of the forest cover), having survived in several refuge areas during adverse periods,

(2) tree species dispersal must be very limited at the scale of the Guineo-Congolian region otherwise gene flow would have homogenized their genetic diversity during periods of maximal forest extension. Therefore, **if the ongoing rapid anthropogenic climate changes result in a**

geographical shift of the potential distribution range of species, there is a high risk that, for most tree species, natural dispersal processes will not be fast enough to allow a range extension in newly suitable areas. Assisted dispersal might be necessary for species that are at risk of extinction in their current distribution area if the later is predicted to become unsuitable under future climate.

Some areas seem to be particularly rich in early diverging lineages within species (e.g. Dauby et al. 2014; Migliore et al. 2019). This is the case of the area surrounding **the Cameroon Volcanic Line** which is also known for its high rate of species endemism. This region **is thus of particular interest for conservation because it harbours a very high phylogenetic diversity and/or phylogenetic distinctiveness, both at the within and among species levels,** constituting an important reservoir of original genetic resources.

Theme 2. – Hidden species diversity and cryptic species: the African forest might contain twice more tree species than currently recognized

Genetic research revealed unsuspected hidden diversity: many taxonomic species comprise several distinct species, potentially doubling the species richness of African trees.

Our studies of genetic diversity within species (see preceding section) allowed to test whether the putative species, as recognized by current taxonomy, really fit the criteria of the Biological Species Concept which is based on reproductive isolation. This led us to reconsider species delimitation in 22 African tree genera. These works were published in 7 articles (Ewédjè et al. 2020; Ikabanga et al. 2017, 2019; Ley &Hardy 2017; Monthe et al. 2018; Lissambou et al. 2018, 2019) and contributed to 5 PhD theses of African students (Donkpegan 2016; Ikabanga 2018; Lissambou, ongoing; Monthe 2019; Tosso 2018).

We detected hidden species when nuclear genetic markers (usually microsatellites) revealed that several genetic clusters were coexisting in sympatry and that no (or very few) admixed individuals occurred (e.g. Ikabanga et al.2017; Lissambou et al. 2019). Such pattern implies that these genetic clusters are reproductively isolated despite the absence of any physical barrier to gene flow, so that the barrier must result from some pre- or post-zygotic incompatibility. These genetic clusters correspond thus to distinct species following the BSC. A re-examination of morphological traits often revealed that these genetic clusters bear diagnostic traits so that species could be delimited using classical morphological approaches, leading to standard taxonomic revisions. In this way the former taxa *Santiria trimera* and *Greenwayodendron suaveolens*, two widespread and abundant trees in Central Africa, have been subdivided in 4 and 5 species, respectively (Ikabanga et al., 2017, 2019; Lissambou et al. 2018).

Several timber tree species were also found to be species complexes, such as *Afzelia bipindensis* (Donkpegan 2016) and *Entandrophragma angolense* (Monthe et al. 2018), which each contain two species following the BSC. In the case of *E. angolense*, the two species detected with genetic markers correspond in fact to *E. congoense* and *E. angolense* which were put in synonymy, indicating that some previous taxonomic revisions were in fact lumping distinct species. However, foresters usually already distinguished *E. congoense* and *E. angolense* by giving them separate commercial names ("tiama noir" and "tiama blanc", respectively), so that forest management plans already accounts for this distinction. This is, however, not the case of *A. bipindensis* which is known under the commercial name "doussié rouge". The two species detected under this taxon name have never been described and morphological analyses did not show differences in traits visible from leaves or twigs (what is generally accessible using herbarium collections) but well in traits from the bark or the trunk (Donkpegan 2016). The diameter structures of the two species also differed significantly, one species being represented by larger trunk diameters than the other one. This has potentially problematic consequences for the management of these species because post-logging recovery rates is estimated from a compound diameter structure mixing the two species while the species with larger diameters is much more exploited than the other one because a much larger proportion of its populations is above the minimum cutting diameter.

A review of population genetics data available for 24 African tree species, as recognized by current taxonomy, showed that 6 of them were certainly composed of several species under the

BSC, and 5 additional ones were probably composed of several species (Table I; O. Hardy, unpublished). The actual number of species would thus increase from 24 to 35 when adopting a conservative estimation (i.e. when both genetic and morphological data indicate that several species occur), but more probably to 48 if genetic data alone is take into account (morphological data have not yet been obtained for all these cases). This highlights that our knowledge of tree species richness in Africa is still incomplete. If we assume that that our sample of 24 taxonomic species is representative of the c. 3000 species currently recognized in tropical Africa, the actual number of species might be closer to 6000.

Table I. List of African tree species currently recognized by taxonomists and for which population genetics data allowed to estimate the actual number (or range of numbers) of species following the Biological Species Concept (BSC).

Taxonomic species	# BSC species	Diagnotic morphological trait
Aucoumea klaineana	1	
Baillonella toxisperma	1	
Distemonanthus benthamianus	1	
Entandrophragma cylindricum	1	
Entandrophragma utile	1	
Erythrophleum ivorense	1	
Greenwayodendron oliveri	1	
Lophira lanceolata	1	
Milicia excelsa	1	
Pericopsis elata	1	
Scorodophloeus zenkeri	1	
Symphonia globulifera	1	
Terminalia superba	1	
Anthonotha macrophylla	1-2	?
Erythrophleum suaveolens	1-2	?
Lophira alata	1-2	?
Milicia regia	1-2	?
Pterocarpus santalinoides	1-3	?
Afzelia bipindensis	2	Yes
Entandrophragma angolense	2	Yes
Staudtia kamerunensis	4-6	?
Santiria trimera	3-5	Yes
Greenwayodendron suaveolens	5	Yes
Khaya anthotheca	6	Yes

Implications for policy making

The **widespread occurrence of cryptic species** (in the sense of distinct species put in synonymy by taxonomists) came as a surprise. It bears important implications for the conservation of biodiversity and the management of exploited species.

For biodiversity conservation, it implies that **some species currently considered as not threatened because of their widespread distribution can in fact be composed of several species, some of which with narrow distribution whose populations might be threatened**. For example, two species were previously considered in the African genus *Greenwayodendron* and they were considered as not threatened following the IUCN criteria given their wide distribution ranges. Our revision based on population genetics data recognized a total of six *Greenwayodendron* species, two of which considered as threatened according to a preliminary assessment because of their narrow distribution ranges (Lissambou et al. 2018). Many cryptic species might be in the same situation.

In managed forests, the occurrence of **unrecognized cryptic species among the exploited timber species**, such as in *Afzelia bipindensis*, **implies that management plans that seek to adjust the level of wood extraction to maintain the resource on the long term may become ineffective**. This is possibly the case of *Afzelia bipindensis* because one of the two species grouped under this name was found to have on average substantially larger trees in south-east Cameroon (Donkpegan 2016), and was therefore much more exploited than predicted by the management plan, questioning the sustainability of its exploitation.

Theme 3. – Time-correlated palynological and biomass burning signatures in lake- sediment records.

Fossil pollen data from east and west of the Congo basin highlight the dominant influence of glacial-interglacial climate cycles on vegetation but also the effects of climate fluctuations occurring at multi-decadal to century time scales, while human impacts seem comparatively weak at the landscape scale or are concentrated in the last few centuries.

Sedimentary records in lakes, swamps and peat bogs from throughout equatorial Africa contain fossil pollen assemblages documenting past changes in the composition of terrestrial vegetation in the surrounding landscape at time scales of 10^2 to 10^5 years. However, hardly any of those records provide a continuous record throughout a complete glacial-interglacial cycle, handicapping direct comparison with genetic data inferring past expansion and contraction of plant distribution ranges. Even at the shorter time scale of the Holocene period (the last *ca* 11,700 years) there are issues of sedimentary hiatuses which complicate accurate dating of pollen-inferred shifts on vegetation composition. Allowing for these difficulties, patterns of long-term vegetation change appear largely synchronous across the region, and testify to the dominant control of climate-driven variation in monsoon intensity and local moisture balance forced by variations in Earth's orbit around the Sun. At the decadal to century time scale, variation in the flux of charcoal particles deposited in lake sediments can provide a detailed record of past changes in biomass burning, i.e. the frequency and/or intensity of fire. Here the methodological bottleneck is the time investment required to analyse sediment records with high temporal resolution such that maxima and minima in charcoal abundance are well-constrained. In this project, sediment records from six lakes throughout Uganda and Kenya and all spanning the last 2000 or more years were analysed at (sub-)decadal resolution, and compared with independent climate proxies. We find that in lowland areas bridging the forest-savannah ecotone, and thus where natural fire occurrence is drought-controlled (i.e., inversely proportional to rainfall), episodes of above- or below-average biomass burning are synchronous between sites throughout most of the last 2000 years; only in recent centuries, sometimes as late as the mid-20th century, does the inverse correlation between biomass burning break down. This means that only in those more recent times, human-induced fires (or fire suppression) have become the dominant control on biomass burning overall. Only at high elevation (>4000 m) in the Rwenzori mountains, episodes of above- or below-average biomass burning are no longer synchronous with those in lowland sites, implying that in those cold tropical environments temperature variation through time influences the relationship between precipitation and biomass burning. More importantly in the context of this project, our results strongly suggest that the cycles of high and low biomass burning in recent millennia which we documented at lowland sites in Uganda also apply to forest-grassland ecotonal areas within the Congo Basin situated further to the west, and that rainforest areas in the Congo Basin experienced the same short-term variability in climate-driven moisture balance. Although natural fire in those rainforests may have been rare or at least infrequent, they would have been exposed to variation in total annual rainfall or length of the dry season synchronous with the variation in fire frequency along the forest margins. This in turn permits direct comparison of the timing of these drought cycles with 1) information on the establishment of forest stands based on inventories of trunk diameter, possibly supplemented with tree-ring based age determination

(WP 1.2); and 2) time series of past moisture-stress variation based on stable-isotope analyses of those tree rings (WP 3.1; Fig. 1).

Theme 4. – Vulnerability of montane ecosystems from western Central Africa: a view from the past

Fossil pollen data of mountain lakes from Western Cameroon show that during the last 90 000 years, forest phases dominated during interglacials while grassland expanded during dry and cold (glacial) periods but without completely excluding trees. The ecological instability of the montane forest contrasts with the apparent stability of lowland equatorial forest, as deduced from the stability of the lower limit of montane forest.

The goal of our research was to look in the past to evaluate the potential in situ adaptation/response of mountain plant associations to changes in environmental conditions and to provide elements to further evaluation of mountain vulnerability. We focused our research on Bambili, Mbi and Monoun, three crater lakes that lie on the Cameroon Volcanic Line between 2273 m and 1090m above sea level in western Equatorial Africa and collected several cores of lake sediment spanning from 90,000 yr BP to the present.

The approach we adopted consisted in determining and counting the pollen grains fossilized in the lake sediments to reconstruct variations in vegetation types (e.g., forests, grasslands) and in diversity over time. Then, beyond the individual behaviour of the plants, it consisted in considering their functional traits, i.e., their physiological response to environmental factors (photosynthetic C3 or C4 pathway of herbaceous plants, evergreen or deciduous trees,...). It was then possible to infer the evolution of the large sets that these functional traits form, the biomes.

These works were published 5 peer-reviewed articles (Izumi & Lézine 2016; Lebamba et al. 2016; Nolan et al. 2018; Verlhac et al. 2018; Lézine et al. 2019), including two in the journal Science (Nolan et al. 2018; Lézine et al. 2019), and a book chapter (Lézine 2017). One additional article is accepted for publication (Lézine et al., accepted) and three articles are still in preparation.

The study shows that Cameroon's montane forests have been susceptible to past climate change with forest phases during humid and warm (interglacial) periods alternating with phases of grassland expansion during dry and cold (glacial) periods (Fig. 3). During the latter, however, forest trees never completely disappeared from the Afromontane forest and remained present as individuals or restricted populations. Downward migration of all the afro-alpine and afro-montane plant types during glacial periods, as shown in the Eastern African mountains, is unlikely in Cameroon. Indeed, unlike for East Africa where mountain glaciers considerably expanded downward by 1000 m or more during glacial periods pushing the low-lying vegetation belts towards lower elevations, there is no evidence of glaciers formation in western Equatorial Africa. The vegetation belts have therefore remained at an altitude roughly equivalent to the current one but the density and geographical extent of forests were however considerably reduced.

We have also shown large vertical movements of the upper limit of the montane forest with dramatic downward shifts during glacial periods, but our most remarkable result was to show that the lower limit of the montane forest remained, on the contrary, remarkably stable over time (Fig.3, middle panel). In other words, the ecological instability of the montane forest induced by successive phases of expansion/contraction contrasted with the relative stability of the equatorial forest block in the lowlands of the Congo Basin.

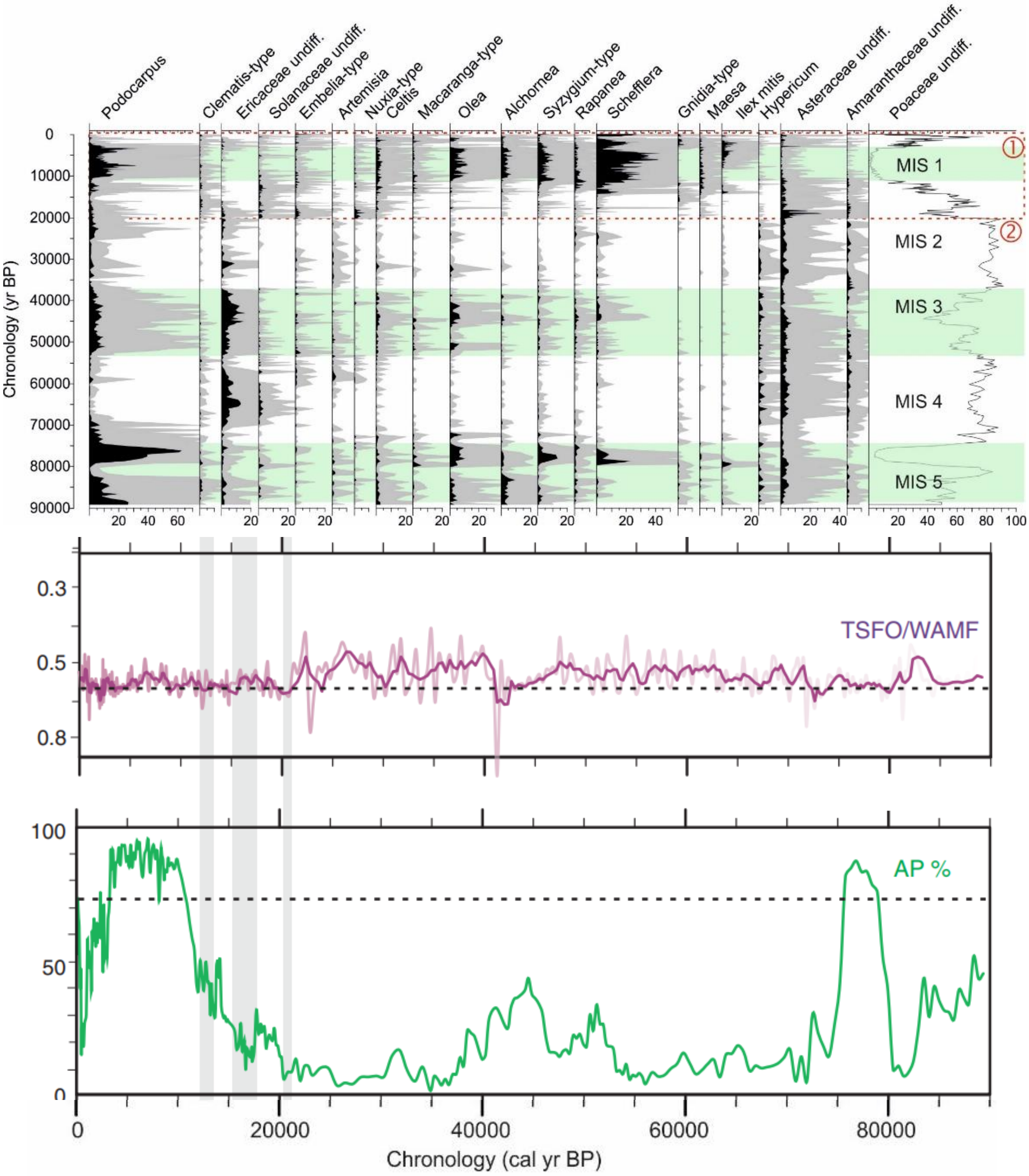


Figure 3. Evolution of the vegetation of equatorial montane forests of western Africa over the past 90 000 years based on Lake Bambili pollen. Upper panel: percentage pollen diagram of selected taxa, where black shading indicates selected taxa versus time, gray shading shows the same results multiplied by 10 for highlighting, and green bands indicate the forest phases during interglacials. Middle panel: lower limit of the Afromontane forest through time estimated by the ratio between lowland tropical seasonal forest (TSFO) and lower level montane forest (WAMF) biomes. Lower panel: tree pollen percentages, where gray vertical bands show, from left to right, the Younger Dryas (YD); Heinrich 1 (H1) events and the Last Glacial Maximum (LGM).

Implications for policy making

Mountain regions are ecologically important. Most of them are recognized as “biodiversity hotspots” and provide critical habitats for many species. They also provide a wide range of ecological services, vital for human well-being: timber, food, fresh water and so on. Although climate change is a global menace, its impact on mountains is especially strong with dramatic implications for human health, safety, and security. The first reason is that high elevation areas experience intensified global change induced warming, and the second reason is that mountains are densely populated, particularly in western equatorial Africa and, in our case, in Cameroon.

Three main implications arise from our findings:

(1) **The relative stability of the boundary between the montane and the lowland forests severely challenges the traditional paradigm of the (even partial) destruction of the equatorial forest block during the last glacial period** (e.g. Maley 1996);

(2) **The ecological instability of the montane forest** may have had a critical influence on the species richness of the Cameroon “diversity hotspot”;

(3) **The Cameroon's mountain forests are particularly sensitive to climate change with a real risk of species extinction due to the combined effect of climate change and recent increase in anthropogenic pressure**.

Theme 5. – Imprint of past environmental changes in the grasslands of Cameroon

Isotopic profile of soil carbon can reveal changes of vegetation type (forests versus savanna) during the late Holocene. In the forest-savanna mosaic of Cameroon, vegetation changes were detected only near the forest margin. The forest degradation documented at the end of the Humid Holocene probably resulted in a change in forest composition and density without replacement of lowland forests by savanna.

The presence of grasslands and wooded grasslands in western Central Africa in areas where climatic conditions would allow the establishment of forests has long questioned naturalists and paleoenvironmentalists. These open landscapes do not occur only at the edge of the lowland forest block such as in center Cameroon to the north or in Congo in the Batéké plateau to the south, they also occupy less extensive areas within the rainforest, such as in the Bakossi region in SW Cameroon. Whether these grasslands and wooded grasslands have a climate or anthropogenic origin is still an unanswered question. We studied the isotopic composition of soil profiles in regions where palynological data are missing.

The end of the Holocene wet period in Central Africa was characterized by the widespread degradation of the equatorial forests, which were replaced either by secondary forests dominated by light demanding trees or by grasslands or wooded grasslands, whatever the altitude. This climate-driven environmental crisis was not restricted to Central Africa and tropical forest elements experienced a widespread regression all over north tropical Africa. In Central Africa, however, an additional driving factor has been evoked: the migration of Bantu farming people from the northern fringe of the forest block, which gradually spread throughout Central Africa as evidenced by numerous linguistic and archaeological studies.

The goal of our research was to know if the present-day “Grassfields” from the southern fringe of the Cameroon volcanic line (CVL) and the wooded grassland/forest mosaic of Central Cameroon originate from the environmental crisis dated from the end of the Holocene Humid Period and to evaluate how deep was the environmental change in the Central African lowlands.

Following an earlier, preliminary study based on six soil profiles (Desjardins et al., 2013), we have extended our dataset which is now composed of 29 soil profiles with the aim of discussing the origin of the present-day landscape of central Cameroon. This work is published in Desjardins et al. (2020).

We found that:

(i) not any marked alteration of the lowland forest massif was observed (Fig. 4). The impact of the environmental crisis that occurred at the end of the Holocene wet period was probably more of a change in forest composition and density than the replacement of lowland forests by a more open landscape dominated by C4 plants. When any, traces of forest expansion/retreat were observed only punctually, at the present-day forest margins (Fig. 4).

(ii) **the present-day wooded grasslands of central Cameroon were never densely forested**. The landscape remained of forest-grassland mosaic-type over the last millennia. Shifts from more to less densely forested landscapes were however observed at dates varying from 3515 ^{14}C BP (from 2000 to 5795 ^{14}C BP) to ca 1955 ^{14}C BP (1430-2480 ^{14}C BP) according to the sites. However, these results have to be considered with caution, as the reported ^{14}C ages represent the average "age" of the soil organic matter, which could account for a mixture of old and young materials. The calendar chronology of these shifts is still in progress.

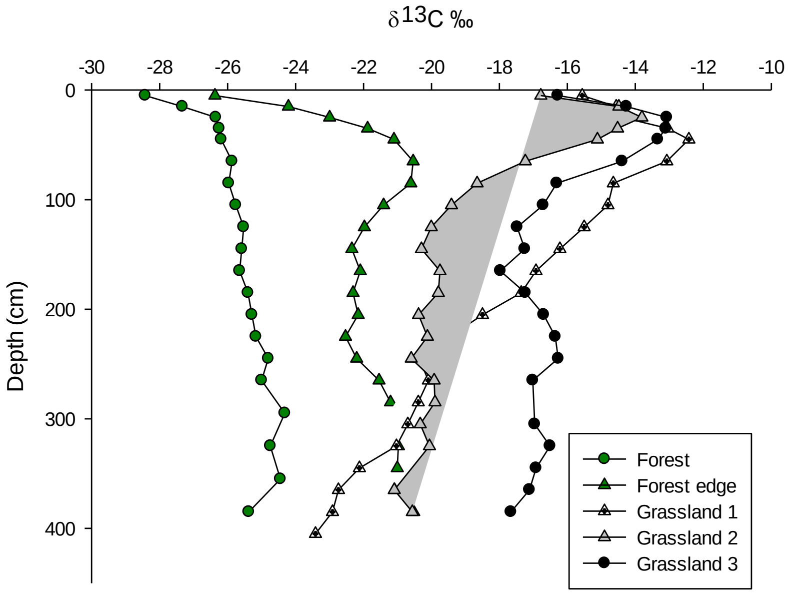


Figure 4. Representative δ^{13}C profiles under forest and grasslands. High and low values indicate the dominance of C4 (savannas) and C3 (forest) plants, and deeper samples represent vegetation in deeper past.

Implications for policy making

Our results suggest some resilience of low- and mid-altitude forest ecosystems which did not experienced such dramatic change compared to the high mountain ones.

Theme 6. – Charcoal analysis reveals the origin of African rainforests: seven centuries of diverging successional pathways shaped present-day compositional and functional diversity.

Mature evergreen rainforests dominated the Congo Basin since AD 1300 until they were heavily disturbed around AD 1650 (e.g. Morin-Rivat et al. 2017). *Subsequent successional pathways over the last three centuries diverged, resulting in several present-day African forest types.*

We untangled past forest history by identifying >4000 charcoal fragments from 40 trenches excavated in 8 permanent forest inventory plots (5 trenches per plot) in the Yoko protected forest, situated in the heart of the Congo Basin (30 km south of Kisangani). Charcoal assemblages from each trench were radiocarbon dated, with two dates performed if two distinct charcoal assemblages were found in a single, stratified trench (total = 50 dates). Charcoal fragments were identified using standard procedures (Hubau et al. 2012) and each fragment was classified according to its light behaviour: (i) pioneers, (ii) non-pioneer light demanders, (iii) shade-tolerant trees. Results are now being interpreted, a publication is in preparation and submission is planned in the course of 2020. Results below are not peer-reviewed and interpretation may change over the course of the review period.

Our results provide insights in (i) the timing of slash-and-burn activities, (ii) which impact these activities had on taxonomic and functional composition of the forest over time and (iii) how well the forests recovered from these disturbances, in terms of speed and composition.

Radiocarbon dates span the periods AD680-880, AD1080-1290 and AD1430-present. We find that all assemblages were dominated by shade-tolerant trees between AD 1300 and 1650 (up to 90% of the identified fragments), while the abundance of forest pioneers and non-pioneer light demanders remarkably increased since AD 1650 (up to 60% of the identified fragments). However, successional pathways since AD 1650 diverged among the plots, resulting in two distinct present-day forest types. A first forest type belongs to the moist equatorial semi-deciduous forests of the alliance *Oxystigmo-Scorodophleion* (Lebrun and Gilbert 1954). These forests are dominated by the shade-tolerant species *Scorodophloeus zenkeri* in the upper strata and *Aidia micrantha* in the lower strata. A second forest type belongs to the secondary alliance *Triplochito-Terminalion* (Lebrun and Gilbert 1954). These forests are dominated by the non-pioneer light-demander *Petersianthus macrocarpus*.

This divergence in successional pathways is a result of differences in disturbance regimes. Present-day *Scorodophloeus* forests were most heavily disturbed between AD 1550 and 1650, resulting in peaking abundances of light-demanders around AD 1650 (up to 80%), which declined ever since, with a present-day abundance of only 20% of the basal area. In contrast, disturbance of present-day secondary *Petersianthus* forests only started since AD 1650, with increasing intensity resulting in increasing abundances of light-demanders (up to 40% of the present-day basal area).

The disturbance factor during the last centuries was most likely human activity, which explains the occurrence of two different successional pathways in forests subject to the same climatic regime and growing in similar edaphic conditions. Slash-and-burn agriculture is a practice that was introduced by Bantu-speaking communities occupying the Congo Basin since 200 BC (Livingstone Smith et al. 2017). While it was most likely only a marginal activity in the first millennium AD, agriculture became progressively more important during the second millennium. We hypothesize that present-day *Scorodophloeus* forests were heavily disturbed through slash-and-burn practices around 400 years ago, but they were abandoned afterwards which allowed recovery of a shade-tolerant tree community. In contrast *Petersianthus* forests were disturbed during a later period, and they were not allowed to regenerate afterwards.

Disturbance was most probably a recurring process in these forests, and the shade-tolerant tree community declined accordingly.

Implications for policy making

Present-day species composition in both forest types is very different from the initial forests that dominated the Congo Basin between AD 1300 and 1650. Back then, the precious timber species *Leplaea thompsonii* was dominant on most of the plots (up to 60% of the fragments), while nowadays it is only a marginal species (only up to 2% of the basal area). This shows that **natural succession after heavy disturbance does not necessarily result in the establishment of the same forest type. Forest types may disappear over relatively short timespans and with them, precious timber species or other valuable ecosystem processes may perish**.

Theme 7. – Dynamic model reconstruction of rainforest distribution change from the Last Glacial period: dispersal, an issue for species survival to climate change

Simulations with a dynamic vegetation model (DVM) allowed reconstructing the glacial refugia of a set of rainforest trees species. However, accounting for seed dispersal, the model projects range shifts by only a few km per 10^3 years, strongly limiting the potential of tree species to follow their optimal climate niche during the rapid climate changes that accompanied the deglaciation.

The biome and species distributions in tropical Africa were simulated by the vegetation model forced by the bias-corrected HadCM3 climatic projections for mid-Holocene and Last Glacial Maximum (LGM). Model validation is hard in the quasi absence of proxy data available over Africa and most of the time limited to the analysis at the biome level (Fig. 5). According to the model, extension of the rainforest is reduced during the dry and cold LGM period and evergreen forest is replaced by deciduous forest or savannah (sub-tropical forest). The model simulates some rainforest suitable areas in Upper and Lower Guinea (separated by the Dahomey Gap) as well as in the Congo Basin, where evergreen forest had certainly found refugia. For mid-Holocene, CARAIB projects a forest expansion in the areas where climate conditions are wetter and not too cold (central and East Africa).

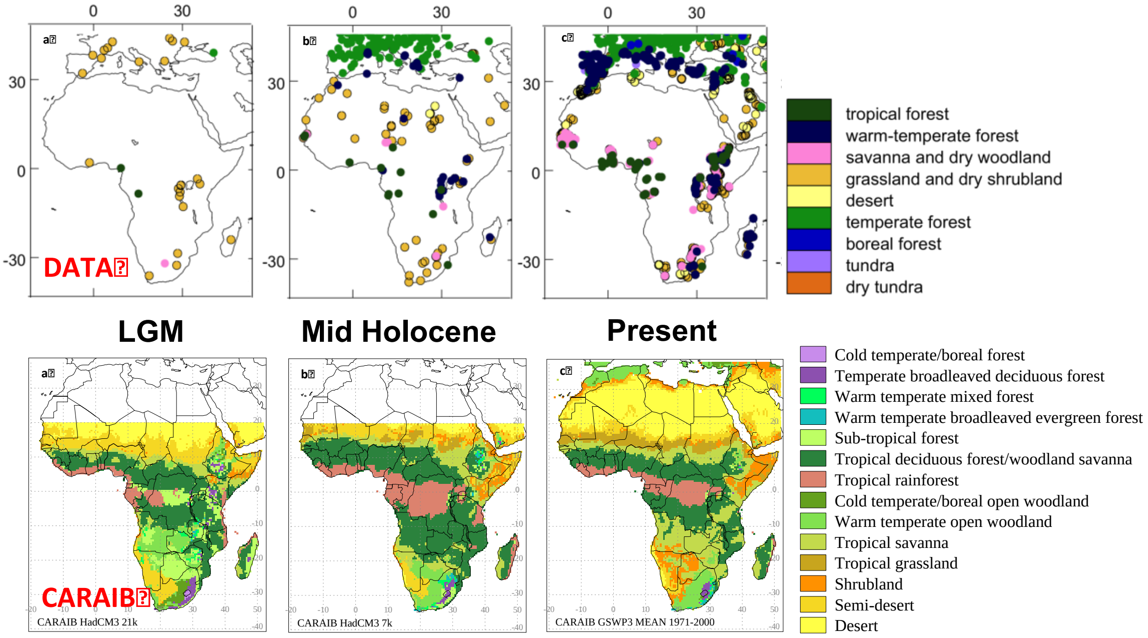


Figure 5. Data and model biome distributions for Last Glacial Maximum (21,000 yr BP), Mid-Holocene (6000 yr BP) and Present-day. Data correspond to Mega-Biome maps from BIOME 6000 (version 4.2; Harrison, 2017). This project has used a standard methodology to map vegetation patterns using fossil pollen and plant-macrofossil data from individual sites

We showed previously (key message 1) that species display genetic signatures dating from 10^4 to 10^6 years. The fragmentation of species distributions simulated by the vegetation model for the Last Glacial Maximum (Fig. 5) is thus too recent to explain alone the observed genetic differentiation. However, LGM simulations can certainly help to understand and explain more ancient climatic episodes (Pleistocene glacial-interglacial cycles), analogous to Last Glacial

Maximum and the following Holocene warming. The repetition of these events led to the present species phylogeography (Fig. 6).

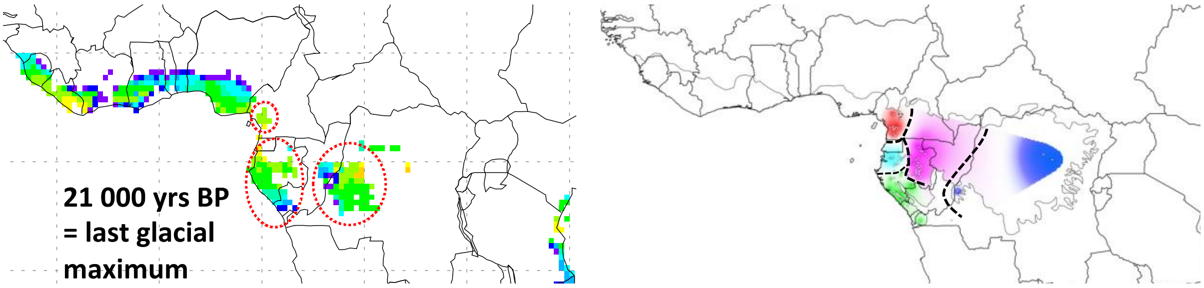


Figure 6. Potential distribution (net primary productivity) of *Scorodophloeus zenkeri* modelled by CARAIB (Dury et al., unpublished) and phylogeographic pattern (genetic clusters; Hardy et al., AETFAT Congress 2017)

Species dynamics from their LGM refugia was tested using a dispersal module developed during the project (O. Hardy, unpublished). On a 200 x 400 km grid (Fig. 7), we assumed the presence of two species categories: 200 species adapted to present-day climate (limited to the coastal grid cells corresponding to some glacial refugia) and 200 species adapted to glacial conditions (distributed everywhere). A common dispersal kernel was inferred from genetic-based observations and corresponds to trees with rather good dispersal capacities (Monthe 2019; Hardy et al. 2019). The resulting average dispersal distance is 1000 m (with 0.1 % of the seeds being dispersed at > 8500 m from their source). After 700 generations (around 21,000 years), species 1 to 200 spread 50 km in average with the occurrence of species patches up to 100 km distance owing to long-distance dispersal events. Species 201 to 400 progressively decreased.

These preliminary results suggest a rather slow species dynamics. While long-distance dispersal events might be underestimated in the simulation, this finding may also suggest that post-glacial recolonization might not have occurred from a few large refuge zones but from a set of local micro-refugia.

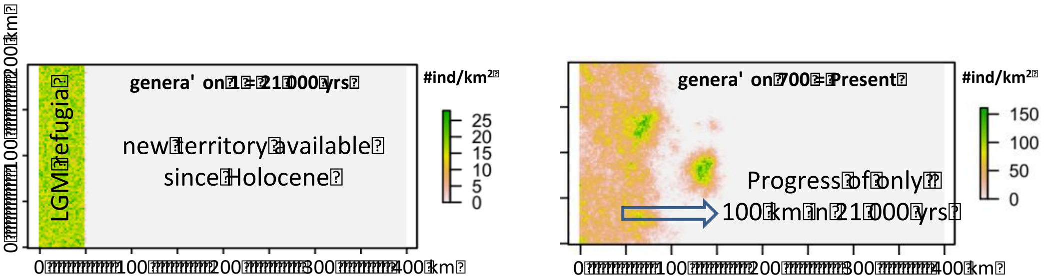


Figure 7. Species dispersal. Preliminary estimates of species spread from Last Glacial Maximum to present on a 200 km x 400 km grid. At the beginning of the simulation, a species, adapted to present-day climate, is limited to the first left 50 km (representing the coastal species refugia). With a generation corresponding to 30 years, 700 generations occur from LGM to present-day.

Implications for policy making

Migrating to sites with appropriate conditions is one way species can cope with a changing environment. However, in the case of African tree species, their long generation time and limited dispersal abilities will strongly limit their capacity to follow their optimal climate niche in the context of the ongoing rapid climate changes resulting from anthropogenic activities.

Theme 8. – *Pericopsis elata*, a highly exploited timber species under CITES convention that requires peculiar management due to its high level of inbreeding

Pericopsis elata *is a highly gregarious timber species, among the most exploited ones in eastern Cameroon, northern Congo and DRC, whose trade is regulated under Appendix II of CITES convention. Tree rings analysis revealed that most stands were aged c. 150 years ago and probably established if large openings, possibly due to slash and burn agriculture. Isotopic signatures in Pericopsis tree rings complemented standard (ring-width) measurements and provided information on stand-scale history (d^{13}C) of individual trees as well as the short-term changes in precipitation (d^{18}O) that characterized the period of forest establishment (ca. from 1860 AD). Genetic data reveals that eastern Cameroon is strongly impoverished in genetic diversity due to founder events, and that the species reproduces often by self-fertilization while it suffers from inbreeding depression. Assisted regeneration methods must be developed given its deficit of natural regeneration and the high pressures on its resources.*

Pericopsis elata is a legume tree species with a discontinuous range throughout West to Central African rain forests. Highly appreciated for its wood, it has nearly vanished from West Africa due to overexploitation and has been integrated into Appendix II of CITES. It remains among the most exploited tree species in eastern Cameroon and DRC.

We used genetic markers previously developed by Micheneau et al. (2011) to study (i) the pattern of genetic diversity in Central Africa, (ii) seed and pollen dispersal in DRC, (iii) the impact of selfing on the fitness of seedlings (inbreeding depression). Part of these works are performed by a PhD student from the University of Kisangani (Dieu-Merci Assumani). Three publications are in preparation. Overall, we found that:

(1) Two well-differentiated genetic groups can be differentiated: (i) a western group encompassing populations from eastern Cameroon, northern Congo-Brazzaville and south-western Central African Republic, and (ii) an eastern group including all populations from central and eastern DRC

(2) Genetic diversity is much lower in the western genetic group, except along the Sangha river, near the border between Cameroon and Congo (Fig. 8).

(3) The species is highly inbred because it often relies on self-fertilization (c. 55% in DRC)

(4) The species suffers from inbreeding depression, as only a portion of the self-fertilized seedlings survive to adulthood (c. 20% of adults result from self-fertilization in DRC)

(5) The majority of seeds disperse over relatively short distances (<100m), contributing to the aggregated distribution of the species and to the strong genetic structure (individuals are highly related up to a distance of c. 1km)

Pericopsis elata was also the focus of tree-ring analyses combined with isotopic measurements. We selected 6 new *Pericopsis elata* discs for additional (d^{18}O and d^{13}C) measurement, including high-quality stem discs covering the last ca. 150 years, and exhibiting common growth patterns to limit micro-site effects (Colombaroli et al., 2016). This dataset included trees which have been dated to 1857, 1872, 1881, 1884, 1896, 1954 (RMCA). The shortest series will be used for correlation with the instrumental data (Colombaroli et al. 2016). Our new series support our previous findings that in the light-demanding *Pericopsis* d^{13}C fractionation is mostly controlled by patch-scale dynamics and microsites conditions, with d^{18}O mostly tracking changes in precipitation. Specifically: 1) the detrended d^{13}C series show asymptotic growth patterns, reflecting the more favourable light conditions in the early stage of the succession, 2) d^{18}O values reflect the wetter conditions around the 1960 as documented in the instrumental record. In addition, they provide information on at least three other episodes of sub-decadal wetter conditions centred around 1885, 1900, 1925 AD.

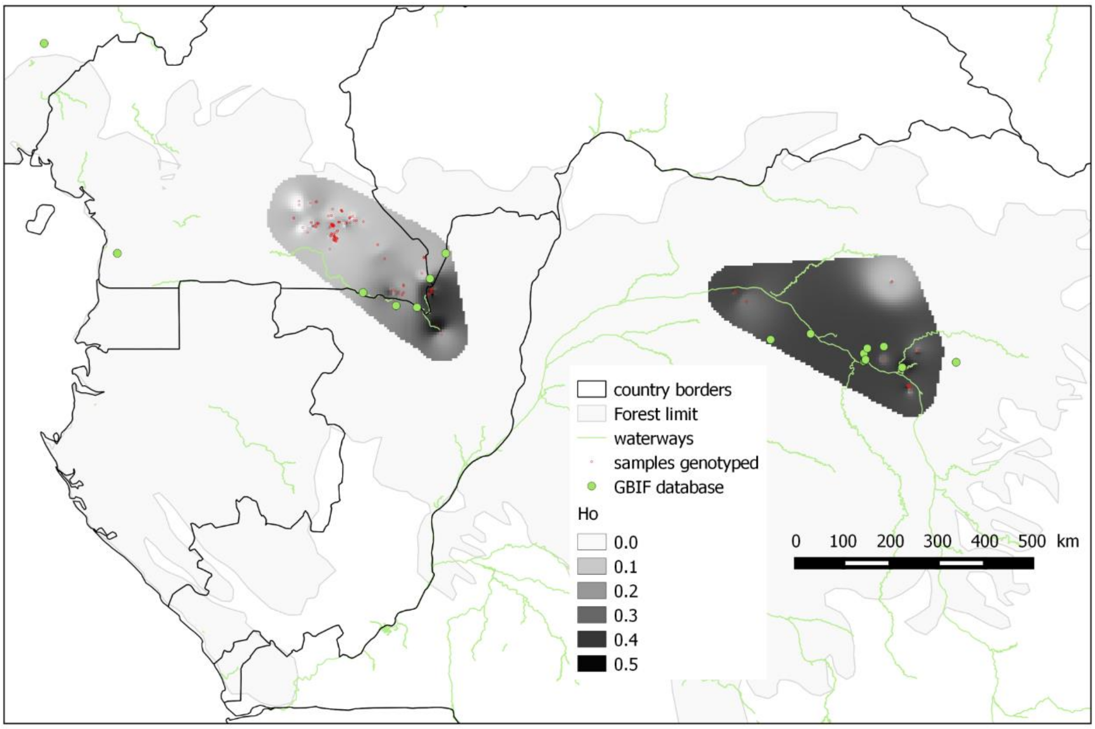


Figure 8. Distribution of *Pericopsis elata* in Central Africa showing gradients of genetic diversity (observed heterozygosity, Ho) at nuclear microsatellite genetic markers. Populations from eastern Cameroon, Northern Congo and Central African Republic display a sharp decay of genetic diversity from the eastern limit (close to Sangha river) towards the western limit, suggesting a recent westward expansion with substantial founding effects. By contrast, populations from DRC have relatively high genetic diversity over the whole range.

Implications for policy making

Being a species listed on Appendix II of CITES convention, *Pericopsis elata* requires special management to guarantee its sustainable exploitation in Central Africa, otherwise its exploitation could become completely banned, as it is already the case in West Africa where *P.*

elata has been largely over-exploited. Suffering from insufficient natural regeneration, the species could benefit from plantation programs. In this perspective, the origin of seeds is very important to consider and our genetic data have important implications.

(1) The western genetic group occurring in eastern Cameroon and northern Congo-Brazzaville appear very impoverished in genetic diversity, probably because of a past westward expansion of the species with founder effects, causing high inbreeding in the western part of its range. As inbreeding depression has also been detected, it is likely that genotypes belonging to this genetic group have a reduced fitness. The only area where relatively high genetic diversity still occurs is along the Sangha river, where the species occurs at relatively low density (J-F Gillet, pers. comm.). Hence, it is essential to conserve the populations occurring along the Sangha river and forbid the exploitation of the species in this area.

(2) A program to collect seeds of *P. elata* along the Sangha river and create conservation orchards would allow to keep genetic material presenting a relatively high genetic diversity that could be used for plantation trials.

(3) The fairly high selfing rate combined with limited seed dispersal cause very spatial genetic structure in this species so that neighbouring individuals tend to be highly related. To avoid planting highly related individuals in plantations, which would result in inbred offspring of low fitness if they mate, it is essential to collect seeds from many seed trees that are at least 1km apart.

Theme 9. – The persistence of carbon in the African forest understory: a small tree is not always a young tree.

Forest giants have long been considered the oldest trees in tropical forests. Combined tree-ring and forest inventory research now shows that small trees in the understory can also be very old, and can even grow older than the big trees. This has important implications for long-term forest management aiming at conserving carbon stocks.

We find that in spite of their much smaller size, mean carbon age in understory trees (74 years) is greater than in sub-canopy (54 years) and canopy (57 years) trees, and similar to carbon age in emergent trees (66 years). The remarkable carbon longevity in the understory results from slow and aperiodic growth as an adaptation to limited resource availability (Bigler 2016)'(Sass-Klaassen 2015). Our analysis also reveals that while the understory represents a small share (11%) of the carbon stock (Bastin et al. 2018), it contributes disproportionally to the forest carbon sink (20%). This novel finding was published in the leading journal *Nature Plants*, as the February 2019 cover story (Hubau et al. 2019). The results were disseminated to a wider audience by publishing an in-depth article in BELSPO's *Science Connection* (June 2019).

To do this, we took advantage of a remarkable rediscovery of a historic forest inventory plot to probe the age structure of African rainforests in a way that has not been possible to date. The Nkulapark plot was established in 1948 in the southwest of the Democratic Republic of the Congo. A total of 6315 trees with diameter at breast height (DBH) >=5cm were tagged and DBH was measured annually for 9 years. In 2014, we rediscovered and remeasured 450 surviving tagged trees, of which 55 were selected to measure growth ring series. We used the grown-in iron nail as a 1948 timestamp, giving accurate estimates of the DBH growth rate (in mm yr^{-1}) and the rate of growth-ring formation (number of rings per year) over a 66 year period for each tree (Fig. 9). The age of each individual tree (in years) was calculated as the total number of rings from pith to bark, divided by the rate of growth-ring formation (number of rings per year). We used the five-class Crown Illumination Index of Dawkins & Field (CII) to compare growth patterns and tree age among the different rainforest strata.

Figure. 9 Keeping up appearances: the small tree is more than 100 years older than the big tree. The small disk belonged to the trunk of an African tree with a diameter of only 7 cm, but with an age of no less than 329 years. The big disc underneath belonged to the trunk of a tree in the crown layer of the same forest. This large tree reached an age of (only) 203 years, and is therefore more than a century younger. Scientists of the RMCA were able to trace the growth speed and the age of the small tree in this photo with precision thanks to the scars of the nail that was knocked into the trunk to attach the tag in 1948. The zone between the black discoloration and the bark is only a few millimeters wide, but the tree took 70 years to form these growth rings.

To test if our findings hold true in a wider geographic context, we compared growth and age patterns among the different forest strata in 23 Central African permanent forest inventory plots. These plots are demarcated rectangles or squares of median size 1 ha where each tree is mapped, tagged and measured according to standard protocols (Lewis et al. 2009). DBH of each tree with DBH>= 10 cm was measured at least twice. We used repeated diameter measurements to estimate the growth rate of each individual tree. We estimated tree age by dividing the final diameter (mm) by the growth rate (mm yr^{-1}), assuming a constant growth rate over the lifetime of a tree (Vieira et al. 2005). Finally, we estimated tree-level mean carbon age as the average age of each year ring, weighted by the carbon content of the ring (Vieira et al. 2005), with a year ring sequence deduced from the growth rate.

Implications for policy making

Tropical forests are essential to regulate the climate by storing excess CO_2 from the atmosphere. They contain half of the biomass carbon on earth. The new knowledge about the age of small trees in tropical forests matters for tropical forest policy aimed at carbon storage. A **small tree contains little carbon, but they live long and are very numerous. Large trees are rarer and have faster life-cycles, but each contains more carbon**. Our work shows that both the large and the small trees contribute to ensure carbon is locked up**. This is an important reminder to scientists and managers to focus on longevity as well as size. One tends to see only the big trees in the forest, but appearances are deceptive.**

Finally, our results suggest that care is required with large-scale modelling of forest carbon accumulation potential and responses to different climate change scenarios (Galbraith et al. 2013). There are two hypothesised responses to increasing atmospheric CO_2 concentrations, possibly explaining the long-term observed AGC-sink in tropical forests (Lewis et al. 2009; Brienen et al. 2015): (i) big trees increasing their asymmetric competition to the detriment of the rest of the stand, or (ii) suppressed trees do best, as they are closer to their light compensation point. Our results show that both scenarios occur in forest stands, with the understory, the canopy and the emergent classes contributing to carbon sequestration, while the sub-canopy classes do not contribute. **Forest and carbon cycle models will need to account for the diversity of carbon age and carbon sequestration potential among the different forest strata.** Recent studies have found that forest structure can be predicted from the characteristics of canopy trees (Bastin et al. 2018;'Lutz et al. 2018), but our results suggest that temporal dynamics differ between forest strata. **The long-term persistence of function depends on smaller trees too, which compared to their stature contribute disproportionately heavily to long-term carbon storage, sequestration, and climate resilience.**

Theme 10. – An end to the sink in intact tropical forests: a blow to global carbon sequestreation

Structurally intact tropical forests sequestered ~50% of global terrestrial carbon uptake over the 1990s and early 2000s, ~15% of anthropogenic CO_2 emissions (Pan et al. 2011). Climate-driven vegetation models used to project that this tropical forest 'carbon sink' will continue for decades (Huntingford et al. 2013). However, recent analysis of ground-based measurements and dynamic vegetation modelling show that the sink in both the Amazonian and African rainforests are declining.

Repeated measurements of stem diameter and height on more than 500,000 trees in Africa and South America allowed researchers at the Africa museum and Leeds University to estimate the evolution of the forest carbon sink over the last 40 years. The results confirm that the World's remaining intact tropical forests have been an active carbon sink over the past three decades. Moreover, this sink remained stable in Africa, while it has been declining since the 1990's in the Amazon (Brienen et al. 2015). First projections based on these measurements suggest that the Amazon sink may decline to zero in the 2030s, while the African sink may persist to the 2060s. These are both much sooner than models previously suggest. This alarming novel research is published in *Nature* (Hubau et al. 2020).

These projections based on measurements are supported by the analysis of climate change impacts on some tropical tree species in central Africa led by the University of Liège using the CARAIB dynamic vegetation model (Dury et al., 2018). For this study, species parameterization was refined from PFT- to species-specific traits, and several climate projections and emission scenarios from the last IPCC report were used to drive the vegetation model. Results highlight the large uncertainties in both the climate projections for the end of the century and in the long-term species physiological response to CO_2 concentration increase.

The analysis of the biomass change over time shows that, in absence of CO_2 fertilization, the biomass of the studied species is projected to decrease, whatever the climatic scenario (the climate model ensemble is shown in Figure 10). Assuming a CO_2 stimulation of growth, biomass of most species might also stop increasing or even decrease after 2070, especially under RCP8.5 scenario (936 ppmv in 2100). Under this scenario, the model projects very contrasted biomass changes between the species.

If we look spatially at the projected changes for the end of the century (Figure 11) for *Ceiba pentendra*), CARAIB projects, in absence of a long-term CO_2 fertilization effect, significant dieback (*i.e.*, amplitude of biomass loss two to three times the biomass variability calculated for the reference 1980-1999 period) over all the conserved distribution. Considering the species ensemble, it means an average biomass loss of −21.2% under RCP4.5 (538 ppmv in 2100) and −34.5% under RCP8.5. Despite a mean biomass increase of 12.2%, assuming a positive feedback of increasing CO_2 on growth does not prevent tree dieback both at the outer limits and in the core of the preserved distributions. This result illustrates the competing effects that climate change and CO_2 fertilization might have.

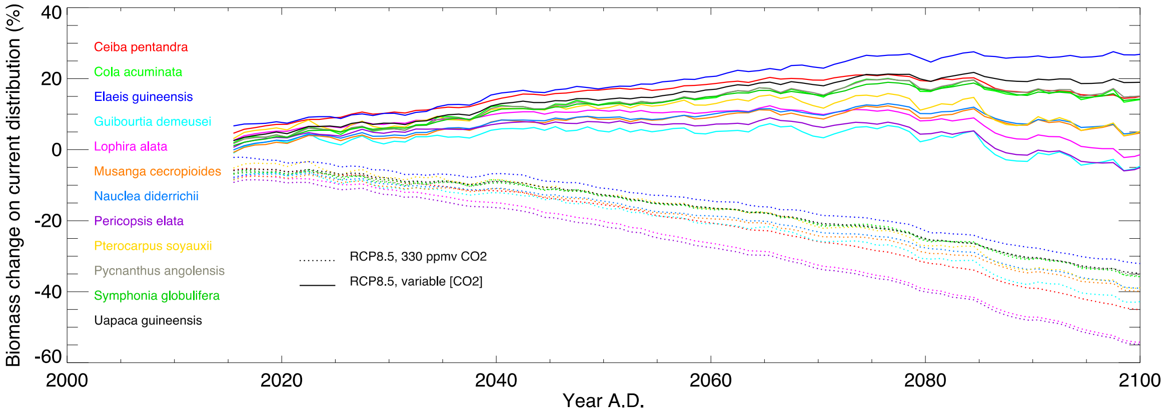


Figure 10. Species biomass change on current distribution over time (from 2015 to 2100) compared to mean biomass for the reference 1980-1999 period (Dury et al., 2018). The values correspond to the ensemble mean of the results obtained with the seven climate projections under the RCP8.5 scenarios, the species-specific morpho-physiological traits, and two configurations of growth response to CO_2, assuming respectively absence of CO_2 fertilization (dotted line) and full stimulation of growth by CO_2 (solid line).

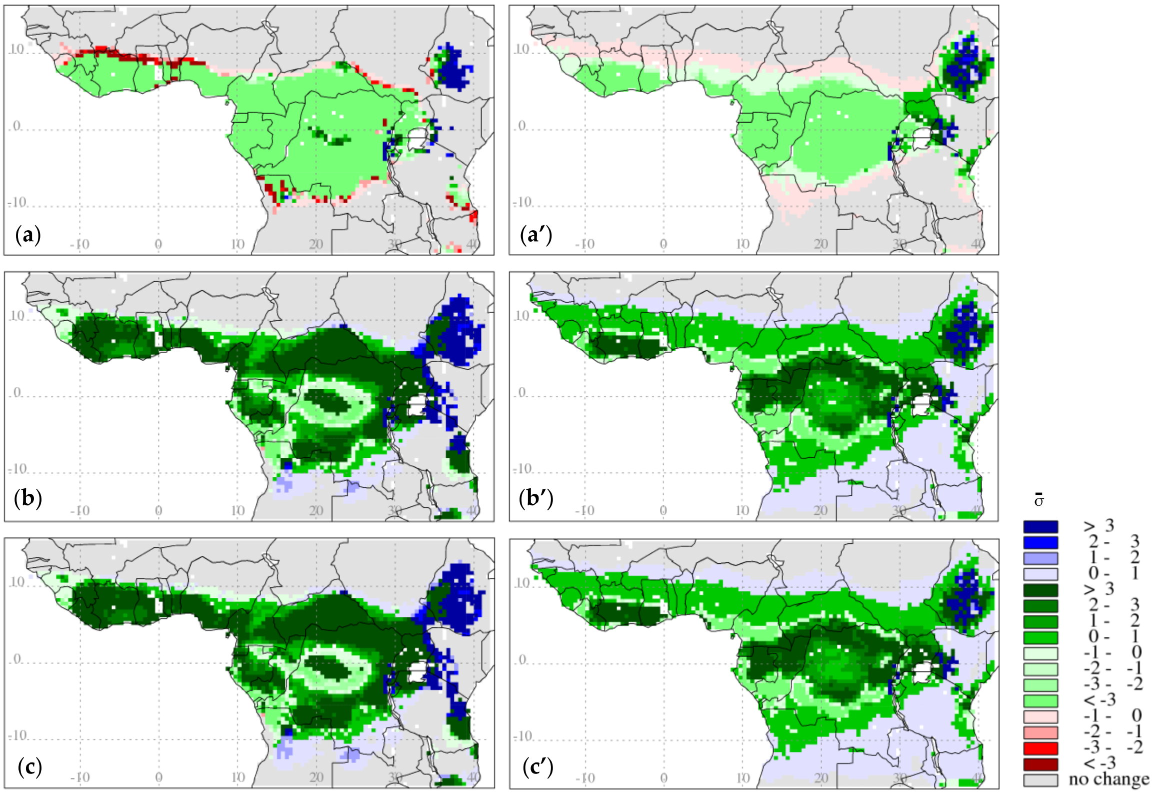


Figure 11. Changes in biomass per unit area (g C m^{-2}) between 2080-2099 and the reference 1980-1999 period (Dury et al., 2018). Biomass change for the species *Ceiba pentendra*. The magnitude of change is expressed as a multiple of the spatial average of the 1980-1999 biomass standard deviation σ (704 g C m^{-2}) over the species current distribution area. Biomasses correspond here to the ensemble mean of the results obtained with the seven climate projections under the RCP8.5 scenario and with species-specific morpho-physiological traits. Three different configurations of growth response to CO_2 are tested: (a) absence of CO_2 fertilization, (b) intermediate response with downregulation of carboxylation capacity, and (c) full stimulation of growth by CO_2. Disappearance of species is indicated in red, expansion in blue and preservation in green. Biomass increase and decrease over the preserved range are respectively in dark and light greens. (a′-b′-c′) the same for *Musanga cecropioides* with a σ of 828 g C m^{-2}.

To give a perspective to the model projections for the future, the simulated change in carbon stock in African tropical forests over historic period has been compared with field plot biomass studies. Lewis et al. (2009) estimated that carbon storage in the biomass of African tropical forests increased by 90.4 g C m^{-2} yr^{-1} from 1968 to 2007 (95% confidence interval: 38.7–116.2 g C m^{-2} yr^{-1}). The vegetation model also simulates a historic carbon sink with gain in biomass falling in the confidence interval of Lewis et al. (2009) but only if a fertilization effect is assumed; otherwise, the model projects biomass decrease during the 1968-2007 period.

Implications for policy making

Intact tropical forests will always be Earth’s biodiversity hotspots and its major stores of carbon. However, they are immediately threatened by deforestation and degradation. Moreover, our results show that the subsidy they provide to humanity via carbon uptake is waning. Our analyses also suggest that climate change impacts in the tropics have been underestimated, as to date no climate-driven vegetation model anticipated rapid near-term reductions in net carbon uptake into intact tropical forests (Huntingford et al. 2013). As such, our findings have significant implications both for refining Earth system models and for the policy pathways needed to limit climate change. **As tropical forests are likely to sequester less carbon in the future than models predict, greater cuts in anthropogenic greenhouse gas emissions will be required to meet any given temperature target**.

Theme 11. – The natural comeback of tropical rainforests in anthropogenic savannas: a boost to global carbon sequestration and biodiversity

Artificial Savanna naturally turns into tropical rainforest when annual burning regimes are discontinued. This is the conclusion of a large-scale experiment carried out in the South-West of the Democratic Republic of Congo. This natural forest regeneration experiment is a model example for reforestation programmes aiming at restoring forest biodiversity and carbon storage capacity in the African tropical forest region.

We designed a forest regeneration experiment within a savanna patch (Manzonzi) in the Mayombe hills, by discontinuing the annual burning regime in an 88 ha exclosure since 2005. A total of 101 permanent inventory plots (40.4 ha) were installed in 2010 and remeasured in 2014. Tree species were classified as savanna or forest specialists. We estimated a forest specialist encroachment rate of 9 stems ha^{-1} yr^{-1} and a savanna specialist disappearance rate of 16 stems ha^{-1} yr^{-1}. Average diameter of forest specialists did not change due to an increasing influx of recruits, while average diameter of savanna trees increased due to decreasing recruitment. Carbon stored by forest specialists increased from 3.12 to 5.60 Mg C ha^{-1}, suggesting a forest carbon recovery rate of 0.62 Mg C ha^{-1} yr^{-1}. Using the average carbon stock of 19 nearby mature rainforest plots as a reference, we estimated a total forest carbon recovery time of at least 150 years (Fig. 12). This novel finding was recently published in *Biological Conservation* (Deklerck et al. 2019).

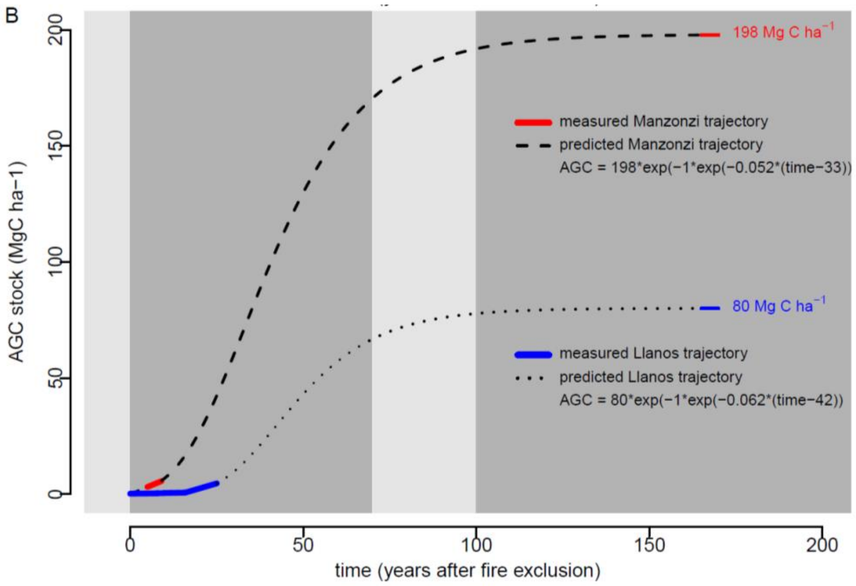


Figure12: Predicted long-term trajectory of aboveground carbon stock recovery. A sigmoid model was parameterised using the observed carbon stock at the 2010 and 2014 censuses, and assuming a final carbon stock of 198 Mg C ha^{-1}, which is the average stock in the reference plots in the Luki reserve. To compare, we also plotted the carbon recovery trajectory of a savanna protection experiment in the Orinoco Llanos plains, Venezuela (monitoring period blue; San Jose et al. (1998).

Implications for policy making

The Manzonzi exclosure is a good example of a natural carbon restoration scheme, without the need of investing in plantations, which come at the cost of reduced biodiversity (Díaz et al., 2009). The trade-off between carbon sequestration versus biodiversity conservation is a well-known issue when developing schemes to **r**educe **e**missions from **d**eforestation and forest **d**egradation (REDD+) (Hirsch et al. 2011; Phelps et al., 2012). Our Manzonzi exclosure shows that **carbon sequestration can go hand-in-hand with biodiversity conservation, by focusing on natural forest regeneration.** REDD+ projects aiming at carbon recovery and biodiversity conservation are a top priority on the agenda of WWF. By the end of 2018, a total of 4396 hectares of savanna exclosures were protected from bush fires to allow natural reforestation (WWF-DRC, 2017; The World Bank, 2018). Such unique collaborations between NGO's, governments and local communities are rare in the tropics, but vital for conservation. Their success largely depends on adequate quantification and long-term prediction of recovery trajectories as presented here.

Another important aspect of the Manzonzi exclosure, is the proximity of the Luki Man and Biosphere reserve. **The fire exclusion and forest recovery experiment represents a direct contribution to the major objective of UNESCO's Man and the Biosphere Programme (MAB), aiming at establishing a scientific basis for the improvement of relationships between people and their environments** (UNESCO 2017). Forest recovery efforts in and around the reserve improve ecosystem functioning, ecological and economical resilience, and ultimately human livelihood (Lamb et al., 2005). In order to fully integrate the Manzonzi fire exclusion experiment into the MAB efforts of the Luki Reserve, several steps will be undertaken through collaboration with WWF: (i) quantify the potential financial benefits of the observed and predicted carbon recovery rates to the local community, (ii) work out possibilities for community-level results-based payments (e.g. through inclusion in official REDD+ systems) and (iii) work out a sustainable way of managing the recovered forests to improve local livelihoods. These steps depend strongly on national and international policy.

Theme 12. – Present realized distribution of African tropical tree species: the importance of competition between species over time

Refining species traits and climatic tolerances in a dynamic vegetation model allows a better representation of competition between species and leads to simulated distributions closer to the realized niches. These results have been presented (François et al., 2019) and are the subject of a publication in preparation.

Large-scale process models that describe the impacts of climate change on African ecosystems generally use the concept of plant functional types (PFTs), which, for tropical forests, are generally very broad classes of plants. They can only provide a very general response of tropical ecosystems to environmental change while individual species with their particular worth show specific responses.

The difficulty of applying DVMs to individual species resides in the importance of specific morpho-physiological traits for optimal model performance; yet, many traits of African tropical tree species remain unknown. Despite these constraints, species characterization in the CARAIB DVM is refined progressively by replacing plant functional type morpho-physiological traits by species-specific traits (specific leaf area, foliage and wood carbon/nitrogen ratios, height, etc.) newly collected or available in the trait databases (Dury et al., 2018). The results clearly show the sensitivity of species productivity to these traits and their intraspecific variations with a direction in NPP change depending on the new combination of traits. This also improves the representation of competition between species in the model.

Model results highlight the importance of competition in species distribution. The species distributions simulated with the dynamic vegetation model were compared to SDM simulations. Both models can reproduce the current distributions rather well. However, the DVM suggests that the present realized distribution of species in Africa results from the competition with other tree species, especially in the lowlands, and that the potential distribution, only climate-limited, might be significantly larger. For example, with a simulation over a thousand years with present climate forcing, *Podocarpus latifolius*, a mountainous species, progressively disappears from the lowlands due to competition and not climate, and converges towards its realized range (Fig. 13). Competition, however, certainly depends on the specific set of tree species that are simulated and there are many more tree species in central Africa.

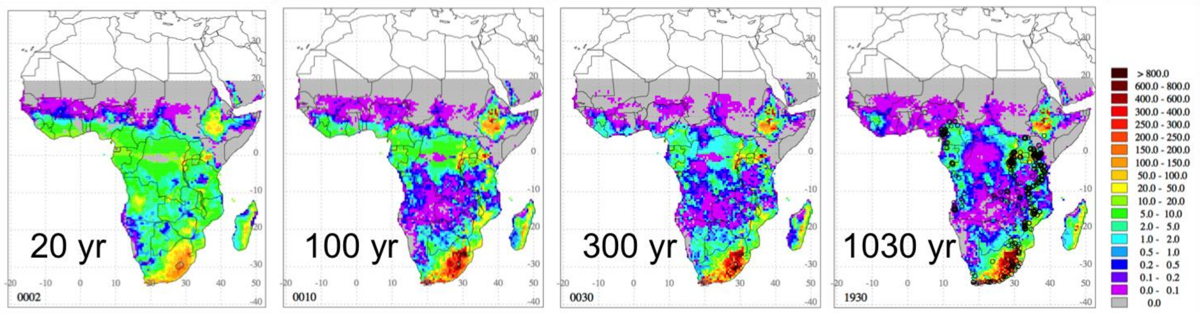


Figure 13. Present-day distribution of *Podocarpus latifolius*. Simulation integration pursued over 1030 years: *Podocarpus* progressively disappears from the lowlands due to competition, and converges towards its realized range. Species presence is evaluated from the effective NPP of species i, frac(i)*NPP(i), among a set of n species, where frac(i) is the fractional cover of the species and NPP(i) is its

net primary productivity per square meter of presence. This provides the realized niche of the species, resulting from the competition with other species (François et al., 2019).

Implications for policy making

Statistical species distribution models are nowadays often used to forecast how climate change will affect the species ranges. However, the output of these models must be interpreted with caution because they implicitly represent the impact of biotic interactions in a statistical way, that is in equilibrium with current climate and CO_2 conditions, while these interactions may differ significantly in a non-equilibrium situation driven by climate and CO_2 change. Mechanistic models integrating the competition between species would be useful to assess such non-equilibrium effects of biotic interactions.

Theme 13. – DVM simulations for the future show significant soil water reduction in central Africa that substantially impact the distribution and net primary productivity of the studied tree species.

What could be the magnitude of tree species responses to climate change in equatorial Africa? To take the range of possibilities the future may hold into account, we used several climate projections produced by global climate models (GCMs) of the Coupled Model Intercomparison Project-Phase 5 (IPCC CMIP5) to 2100 time horizon under two Representative Concentration Pathways, RCP4.5 and RCP8.5. These works were published by Dury et al. (2018).

The differences between the climatic scenarios from seven GCMs under two RCPs and three CO_2 configurations highlight the large uncertainties in the future of African tropical tree species. They are first related to uncertainties in the climatic scenarios. The GCMs selected for the study vary greatly in their projections of future precipitation although several of them similarly project increases in precipitation in eastern Africa and decreases in western Africa. Soil water content relative anomalies (increase factor, e.g., 0.5 = reduction by a factor of 2, 1 = no change, 2 = doubling) projected by the vegetation model (Fig. 14) show that the temperature rise emphasizes soil water deficits, even in areas where climatic models project unchanged or increasing rainfall.

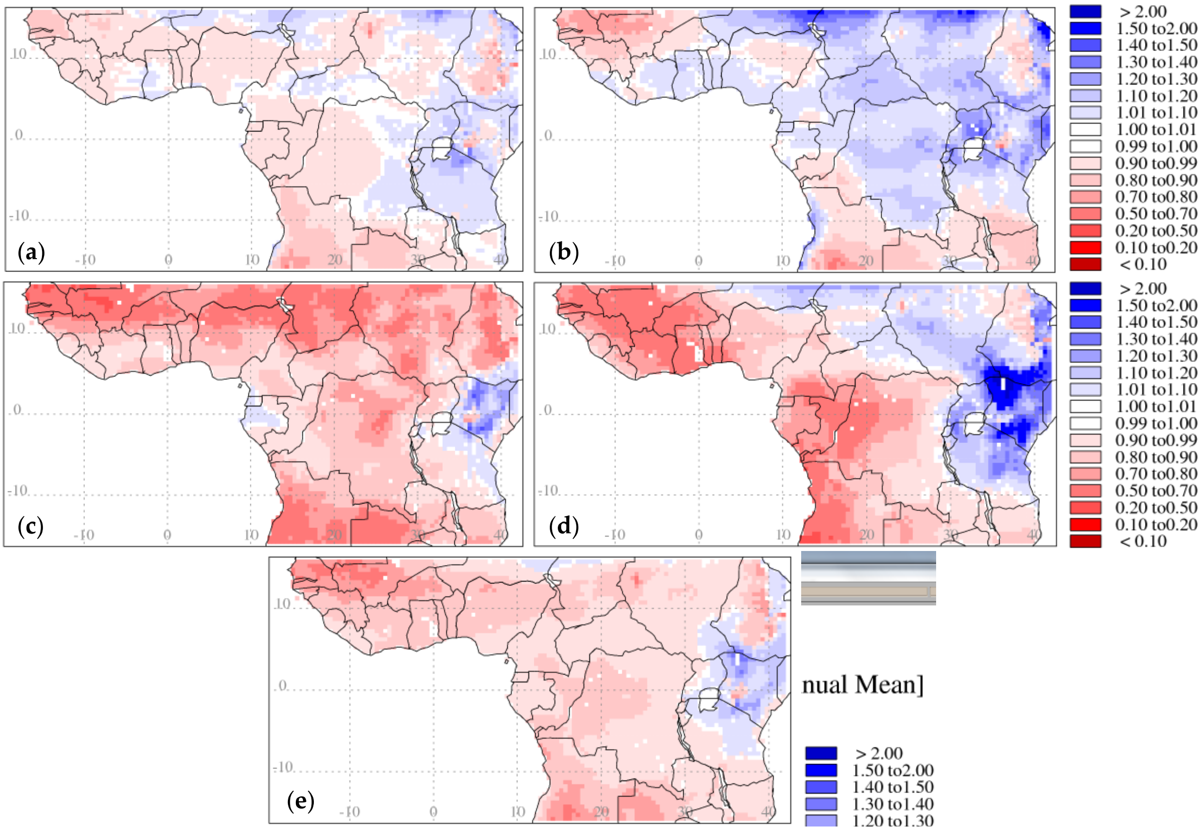


Figure 14. Increase factor of soil water (i.e., the ratio of average available soil water amounts between the annual average over the 2080-2099 period and the reference 1980-1999 period), under the RCP8.5 scenario and a variable CO_2 mixing ratio, for (a) the best ranked model CNRM-CM5, (b) the most humid model CESM1-BGC, (c) the driest model CSIRO-Mk3.6.0, (d) the warmest model CanESM2 and (e) ensemble mean of the results obtained with the seven climate projections (Dury et al., 2018).

The study focuses on 12 species (trees and palms) known to be widely used by local populations in central Africa. In analogy with species statistical model method of setting a threshold under which one considers the probability of species presence to be too low, we set the presence threshold of presence at 100 g C m^{-2} yr^{-1}. Simulated changes in species productivity are presented via the analysis of changes in species distribution.

Projected changes in species distribution vary greatly with the general circulation model (GCM) and, to a lesser extent, with the RCP concentration pathway. The question about long-term plant response to increasing CO_2 concentrations also leads to contrasting results. In absence of fertilization effect, species are exposed to climate change and might lose 25% of their current distribution under RCP8.5 (12.5% under RCP4.5), considering all the species and climatic scenarios (Fig. 15). Potential range expansions, unpredictable due to migration limitations, are too limited for offsetting range contraction. By contrast, if the long-term species response to increasing [CO_2] is positive, the range reduction is limited to 5%.

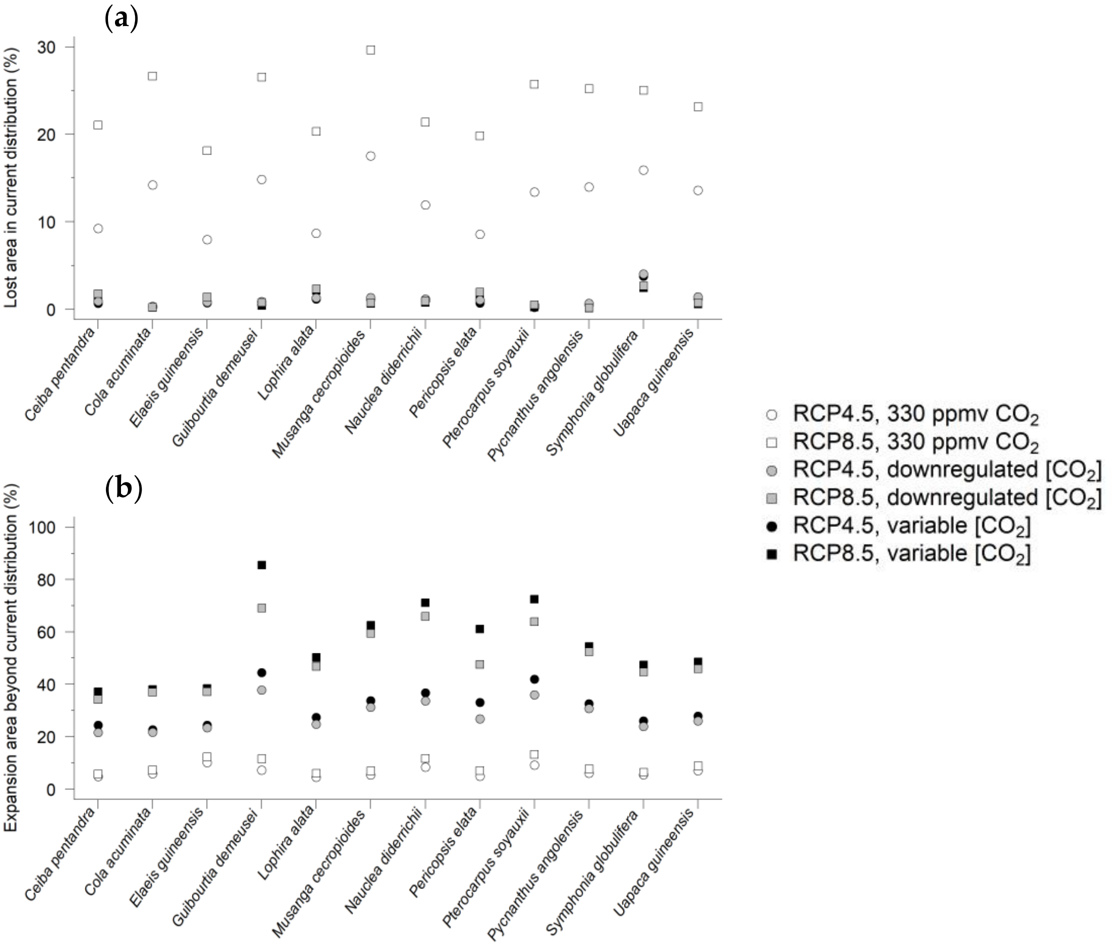


Figure 15. Changes in species distribution between the 2080–2099 period and the reference 1980–1999 period. (a) Lost area in the species current distribution and (b) expansion area beyond the current distribution, considering NPP values above the presence threshold of 100 g C m^{-2} $year^{-1}$. The values correspond to the ensemble mean of the results obtained with the seven climate projections under the RCP4.5 (squares) and RCP8.5 (circles) scenarios, and three CO_2 response configurations assuming respectively absence of CO_2 fertilization [330 ppmv] (white), an intermediate response to CO_2 assuming downregulation of carboxylation capacity [downregulated] (grey) and full stimulation of growth by CO_2 [variable] (black), and species-specific morpho-physiological traits.

This zoom on individual species confirms that individual species respond differently to new climatic and atmospheric conditions, which may induce a new dynamics of competition in the ecosystem (*cfr* previous key message). But, the traits values used in this study are measured under current climate conditions and, under influence of climate change, acclimation of these traits may occur. For example, rooting depth could be a major determinant of how tropical trees will fare during extreme droughts. Assumptions on the physiological responses of species to new climatic conditions thus remain necessary.

Implications for policy making

In tropical Africa, how climate change will affect precipitations in the future remains uncertain given the discrepancies observed between general circulation models. It is therefore still difficult to predict reliably how plant species will respond to these changes. Another difficulty is linked to evaluating the long-term effect of CO_2 fertilization, i.e., the down-regulation of the photosynthetic capacities associated with the acclimation of the species to higher CO_2 levels. Large uncertainties remain on the intensity of this down-regulation, while vegetation models appear very sensitive to it.

Additional output of AFRIFORD:

Training of people

A three-week training of 20 African researchers has been organized in march-april 2016 as a collaboration between the Wood biology team of the RMCA and the "Centre de Recherche en Sciences Naturelles" (CRNS) in Lwiro, near Kahuzi-Biega national Park (DRCongo). The focus was on wood anatomy, dendrochronology, dendrology, forest inventory and sustainable forest management. Theory courses were combined with field courses and the trainees assisted in collecting forest inventory data of three newly installed 1-ha forest plots. They also assisted in collecting charcoal fragments from three profiles around the plots. A selection of the 20 students trained at Kahuzi-Biega were invited for further training at the RMCA in the course of 2016. From these, the best student was selected and given a PhD scholarship.

PhD theses of African students

AFRIFORD has contributed to the formation of African students in the context of their PhD theses:

Armel DONKPEGAN, "Origine, évolution et diversité des espèces au sein du genre *Afzelia* Smith : implication pour la conservation des ressources forestières en Afrique tropicale", 2016, ULg

Félicien Dji-ndé TOSSO, "Biodiversité, origine et évolution des espèces au sein du genre *Guibourtia* Benn – approches génétique et écophysiologique", 2018, ULg

Boris DEMENOU, "Etude de la variabilité génétique et de la phylogéographie d'espèces rélictuelles de la forêt Guinéo-Congolaise dans la Dahomey-gap: implications pour une conservation durable des forêts humides semi-décidues", 2018, ULB

Davy IKABANGA, "Taxonomie et génétique d'espèces d'arbres des forêts tropicales d'Afrique - le cas du complexe *Santiria trimera* (Burseraceae)", 2018, Université des Sciences et Techniques de Masoku (Gabon)

Franck MONTHE KAMENI, "Le genre *Entandrophragma* (Meliaceae) comme modèle d'étude de la diversité et de l'évolution des forêts tropicales humides Guinéo-Congolaises", 2019, ULB

Dieu-Merci ASSUMANI, "Mécanismes de régénération et dynamique spatiale de *Pericopsis elata* (Harms) Van Meuwen (Fabaceae), arbre de forêt tropicale à répartition agrégée", ongoing, Université of Kisangani (RDC)

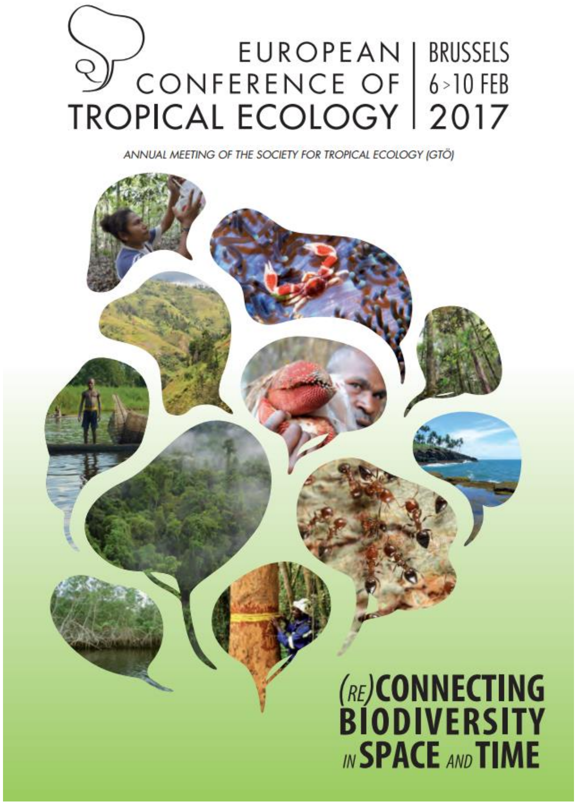
Brandet LISSAMBOU, "Structuration de la diversité génétique du genre *Greenwayodendron* dans les forêts tropicales d'Afrique", ongoing, Université des Sciences et Techniques de Masoku (Gabon)

AFRIFORD also contributed to the postdoctoral formation of Eben-Ezer Ewèdjé (Ecole Nationale Supérieure des Biosciences et Biotechnologies Appliquées ENSBBA/Dassa-Zoumé / UNSTIM-Abomey, Benin).

5. DISSEMINATION AND VALORISATION

AFRIFORD has generated a large body of scientific results, often in interactions with other related projects, which are reported so far in **40 articles published in peer-reviewed scientific journals** (listed in next section), including in *Nature* (Hubau et al. 2020) and *Science* (Lézine et al. 2019). The scientific results have also been reported in multiple international conferences (list in next section).

On 6-10 February 2017, we organized the "**European Conference of Tropical Ecology**" (which was also the 3^{0th} Annual Conference of the Society for Tropical Ecology) in Brussels, with 365 participants from 37 countries. During this 4-days conference, 97 posters and 259 oral communications were presented in 25 sessions. The abstracts are published in a >500pp. abstract book. Different members of AFRIFORD organized 6 sessions on the following themes: S1 - Traits and functions in the tropics, S3 - Gene flow in the tropics, S5 - Species delineation in the tropics, S6 - Tropical forest modelling, S16 - Palaeoecology of tropical ecosystems, S20 - Integrative tropical ecosystems dynamics.



Communicating research results to policymakers:

Anne-Marie Lézine participated to the **COP 21** manifestations in Paris (2015) through the Société Géologique de France and the International Scientific Conference, presenting "Our Common Future under climate Change" and "Sur l'homme ou le climat, ce que nous apprennent les paléodonnées d'Afrique tropicale".

On 27 November 2018, members of AFRIFORD organized the **Scientific Side Event to the 18th meeting of parties of the Congo Basin Forest Partnership (CBFP)** at the Africamuseum. Oral and poster presentations allowed to divulgate scientific research to a broader audience of policy makers. One of the three scientific session was chaired by Hans Beeckman: "Session 1 : The effects of climate change on tropical forest structure and dynamics", where the following talks were directly related to the output of AFRIFORD:

- Wannes Hubau "Carbon sequestration and persistence in Central African forests"
- Olivier Hardy "Understanding the past to predict the future – How vegetation has responded to past climate change in Central Africa"
- Emmanuel Kasongo "Long term analysis of rainfall and temperature data of a Congolese intact forest (1980-2016)"

On 29 April 2019, Olivier Hardy presented the output of AFRIFORD in Kisangani (DR Congo) during the **UNIKIS-CIFOR Science Week** # 6 : "Understanding the past to predict the future – How vegetation has responded to past climate change in Central Africa"

Scientific vulgarization was published in BELSPO's Science Connection: Hubau et al. (2019) De kleine bomen door het bos zien / Les petits arbres sortent de l'ombre des forêts. *Science Connection*, 60, p30-34.

Moreover, the publication of two keynote articles (Hubau & de Mil et al. 2019 *Nature Plants* and Deklerck et al. 2019 *Biological Conservation*) received substantial **media coverage**:

- Knack
- Phys Org
- Daily Science
- Belga (fr)
- Belga (nl)
- Het laatste Nieuws
- La Libre Afrique
- La tempête
- Provinces 26 RDC
- Science Trends
- The Belgian Scientist

Finally, a website presents the project: https://www2.ulb.ac.be/facs/sciences/afriford/

Genetic and paleoecological signatures of African rainforest dynamics:
Pre-adapted to change?

6. PUBLICATIONS RESULTING FROM AFRIFORD

Peer-reviewed publications

Submitted, in review, accepted

Angoboy Ilondea, B., De Mil, T., Chantrain, A., Hubau, W., Van Acker, J., Van den Bulcke, J., Fayolle, A., Beeckman, H. The role of the rainforest understory in carbon sequestration: complementary evidence from repeated diameter measurements and dated wood. *Dendrochronologia* (in review).

Lézine, A.-M. Are *Podocarpus* populations of Western Central Africa doomed to disappear? *Quaternary Science Reviews* (in review).

Izumi, K.,Lézine, A.M. Pollen-based climate reconstruction at western and central Equatorial African mountains during the last deglaciation. *Quaternary Science Reviews* (submitted)

Lézine, A.M., Izumi, K., Achoundong, G. (2021) Mbil Crater (Cameroon) illustrated the relations between mountain and lowland forests over the last 15,000 years in Western Equatorial Africa. *Quaternary International* (accepted).

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Other publications

Presentations at international conferences

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François, L., Henrot, A.-J., Dury, M., Hambuckers, A., Lézine, A.-M., Migliore, J., Paillet, M., Trolliet, F., Hardy, O., and Cheddadi, R. (2019). Comparing statistical and process-based models to calculate the distribution ranges of Podocarpus and Afrocarpus trees in central Africa and assess their response to climate change. VULPES Final meeting, Cuenca, Ecuador, March 11-15, 2019.

Hardy OJ, J. Duminil, K. Daïnou, F. Monthe, B. Delaide, H. Hainaut, P. Gillet, D. Mendene, D. Kombi, J.-L. Doucet. "Seed and pollen dispersal in Guineo-Congolian canopy tree species – insights from genetic markers in multiple species" Annual Conference of the Society for Tropical Ecology, Zurich (Switzerland), April 8 2015.

Hardy OJ, Duminil J, Daïnou K, Ikabanga DU, Piñeiro R, Monthe Kameni F, Lissambou B-J, Ewedjé E-E. "The prevalence of cryptic plant species in African rain forest trees - Insights from population genetics approaches" Annual Conference of the Society for Tropical

Ecology, Göttingen (Germany), February 2016.

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ANNEXES

ANNEX 1: copy of the publications (zip file with pdf of articles)