ABSTRACT

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

Context

Tropical rainforests are the terrestrial biome with the greatest diversity of plant and animal species. Long-term stability against environmental change has been considered for long as a prime cause of this remarkable biodiversity. 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. The evolutionary and environmental history of the Central African rainforest, in particular, is barely known while its remarkable biodiversity is severely threatened.

Objectives

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, and how African forests are affected under current anthropogenic climate changes. Signatures of past climate change in Central Africa were investigated over a range of time scales, combining paleo-vegetation proxies, wood biology, genetic variation and vegetation modelling, from the perspective of forest trees. The specific scientific objectives of this project were to:

1) Understand the processes leading to the diversification/differentiation of African rainforest tree biodiversity at inter-specific and intra-specific levels;

2) Document the main climatic and anthropogenic perturbations which affected past vegetation dynamics in the Congo basin for a range of relevant time scales;

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

Main conclusions

- Genetic data show that most African forest tree species are not homogeneous entities but contain genetically differentiated populations, separated by (ancient) biogeographic barriers. These genetic signatures of past population fragmentation and demographic changes are dated from tens of thousands to millions of years ago. This highlights the very long-term impact of past environmental changes on species genetic variation and the likely role of glacial-interglacial cycles throughout the Quaternary in generating recurrent fragmentation of forest cover, not only at the peak of the most recent glaciation period (i.e., during the Last Glacial Maximum). These results illustrate the resilience of tree species, which survived in several refuge areas during adverse climatic periods, but they also point to their limited dispersal abilities for recolonization. Our data also show that the area surrounding the Cameroon Volcanic Line is an important reservoir of original genetic resources (high phylogenetic distinctiveness) for biodiversity conservation.

- Simulations with the dynamic vegetation model CARAIB allowed reconstructing the glacial refugia of a set of rainforest trees species. However, accounting for seed dispersal, the model

projects range shifts of only a few km per thousand years, strongly limiting the potential of tree species to follow their optimal climate niche under rapid climate change. Therefore, if ongoing rapid anthropogenic climate change shifts the potential distribution range of species substantially, most tree species will not be able to disperse fast enough into newly suitable areas. Assisted dispersal might be necessary for species that are at risk of extinction in their current distribution area.

- Genetic research also revealed unsuspected hidden diversity: many tree species comprise several species according to the Biological Species Concept, potentially doubling the species richness of African trees. We also show that genetic markers can guide taxonomic works to identify diagnostic morphological characters, reconciling classical taxonomy with genetic data. The abundance of cryptic species has important implications for conservation. First, some species apparently unthreatened following the IUCN criteria due to their large distribution range are composed of several narrowly distributed species. Second, forestry management rules to exploit sustainably timber species are ineffective if species with distinct biological characteristics are confounded.

- Time-correlated palynological signatures in lake sediments from highlands to the east and west of the Congo basin spanning the last 10^5 years highlight the influence of glacial-interglacial climate cycles on vegetation but also the effects of climatic fluctuation occurring at multi-decadal to century scales, while human impacts seem relatively weak in comparison or concentrated within the last few centuries.

- Fossil pollen data of mountain lakes from western Cameroon show that during the last 90,000 years, forest phases dominated during interglacial periods while grassland expanded during the drier and cooler glacial periods but without completely excluding trees. The ecological instability of montane forest contrasts with the apparent stability of lowland equatorial forest in this area, as deduced from the stationarity of the lower limit of montane forest. The palynological records show that Cameroon's mountain forests, already recognized as "biodiversity hotspots", are particularly sensitive to climate change with a real risk of species extinction due to the combined effect of climate change and increase in human pressure.

- Isotopic profiles of soil carbon ($\delta^{13}C$) revealed changes of vegetation type (forests versus savannah) during the late Holocene. However, in the forest-savannah mosaic of Cameroon, vegetation changes were detected only near the modern-day forest margin. Therefore, the forest degradation documented at the end of the early-Holocene African Humid Period probably resulted in a change in lowland forest composition and density rather than large-scale replacement of forest by savannah. These results suggest relatively high resilience of low- and mid-altitude forest ecosystems, at least in comparison with montane forest.

- Soil charcoal analysis combining species identification and radiocarbon (^{14}C) dating revealed compositional changes of African rainforests during the last millennium. In particular, mature evergreen rainforests dominated the Congo Basin since AD 1300 until they were heavily disturbed from around AD 1650. Subsequent forest successional pathways over the last three centuries diverged, probably as a result of the spatiotemporal heterogeneity of slash-and-burn agriculture, resulting in several present-day African forest types. This shows that natural succession after heavy disturbance does not necessarily evolve towards a single forest type. Forest types may disappear over relatively short timespans and with them, precious timber species or other valuable ecosystem processes may perish.

- Among economically valuable African timber species, *Pericopsis elata* ('afromosia') received special attention, being one of the most exploited species and of which the trade is regulated under Appendix II of the CITES convention. Tree-ring analysis revealed that most stands were aged c. 150 years and were probably established in large canopy openings created by slash-and-burn agriculture. Isotopic signatures ($\delta^{13}C$) in growth rings provided information on stand-scale history and short-term changes in precipitation. Genetic data reveal that the *Pericopsis elata* population in 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. To ensure sustainable exploitation, assisted regeneration methods must be developed given the deficit of natural regeneration and the high pressures on natural populations.

- The potential of tropical forests for carbon storage is a key issue in climate-change science. Giant forest trees have long been considered the oldest trees in tropical forests. However, 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 forest management aiming at conserving carbon stocks because both biomass and longevity matters for long-term carbon storage. Hence, forest and carbon-cycle models need to account for the diversity of carbon age and sequestration potential among forest strata, given that smaller trees contribute disproportionately to long-term carbon storage, sequestration, and climate resilience, compared to their stature.

- By analysing tree growth over 40 years, tropical forests have been shown to sequester an amount of carbon equivalent to c. 15% of anthropogenic CO_2 emissions during this period. However, our projections based on tree growth measurements suggest that the Amazon sink may decline to zero in the 2030s, while the African sink may persist to the 2060s. These results are also supported by CARAIB simulations highlighting the current importance of CO_2 fertilization. As tropical forests are likely to sequester less carbon in the future than predicted by current climate models, greater cuts in greenhouse gas emissions will be required to meet any given temperature target.

- While the carbon-sink effect of existing African forests is reducing, our research shows how the natural comeback of tropical rainforests in anthropogenic savannahs when annual burning regimes are discontinued can boost both global carbon sequestration and biodiversity. In the southwestern DR Congo, the large-scale Manzonzi fire exclusion experiment 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.

- To forecast how Congo rainforest vegetation and its constituent tree species will respond to current climate changes, the CARAIB dynamic vegetation model allows to integrate species traits and climatic tolerances to better model competition between species and predict their realized niches. Acquiring appropriate functional traits remains, however, challenging given the high species richness of African forests. Moreover, climate projections for tropical Africa can differ substantially among different general circulation models and scenarios, in particular for water availability. Therefore, it remains difficult to predict reliably how plant species will respond to ongoing climate changes.

Overall, AFRIFORD has contributed to (i) link researchers from diverse backgrounds in a multidisciplinary project, (ii) the formation of young researchers (notably from Africa), and (iii)

the publication of 40 scientific articles. We describe implications of policy makers in a set of 13 themes.

Keywords:
African forest dynamics, climate change, carbon sequestration, Congo Basin, genetic diversity, paleovegetation, Quaternary