



The demographic and adaptive history of central African hunter-gatherers and farmers

Etienne Patin^{1,2,3} and Lluís Quintana-Murci^{1,2,3}

Central Africa, a forested region that supports an exceptionally high biodiversity, hosts the world's largest group of hunter-gatherers, who live in close proximity with groups that have adopted agriculture over the past 5000 years. Our understanding of the prehistory of these populations has been dramatically hampered by the almost total absence of fossil remains in this region, a limitation that has recently been circumvented by population genomics approaches. Different studies have estimated that ancestors of rainforest hunter-gatherers and Bantu-speaking farmers separated more than 60 000 years ago, supporting the occurrence of ancient population structure in Africa since the Late Pleistocene. Conversely, the Holocene in central Africa was characterized by large-scale population migrations associated with the emergence of agriculture, and increased genetic interactions between autochthonous rainforest hunter-gatherers and expanding Bantu-speaking farmers. Genomic scans have detected numerous candidate loci for positive selection in these populations, including convergent adaptation for short stature in groups of rainforest hunter-gatherers and local adaptation to endemic malaria in western and central Africans. Furthermore, there is recent increasing evidence that adaptive variation has been acquired by various African populations through admixture, suggesting a previously unappreciated role of intraspecies gene flow in local adaptation. Ancient and modern DNA studies will greatly broaden, and probably challenge, our view on the past history of central Africa, where introgression from yet uncharacterized archaic hominins and long-term adaptation to distinct ecological niches are suspected.

Addresses

¹ Unit of Human Evolutionary Genetics, Department of Genomes and Genetics, Institut Pasteur, 75015 Paris, France

² Centre National de la Recherche Scientifique (CNRS), UMR2000, 75015 Paris, France

³ Center of Bioinformatics, Biostatistics and Integrative Biology, Institut Pasteur, 75015 Paris, France

Corresponding authors: Patin, Etienne (epatin@pasteur.fr), Quintana-Murci, Lluís (quintana@pasteur.fr)

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Introduction

The central African belt—a vast territory that extends from the Congo Basin in its western part to Lake Victoria in its easternmost part—is mostly covered by dense rainforests and supports one of the highest levels of biodiversity worldwide. This region is key to understand African prehistory, population structure and dynamics as it harbours both the largest living group of active hunter-gatherers, the rainforest hunter-gatherers, as well as Bantu-speaking, agriculturalist communities [1–3]. These two groups differ not only in their subsistence patterns (i. e., broadly, although not exclusively, hunting and gathering vs. farming) but also in their lifestyle, ecologies and exposure to environmental pressures [4] and diseases [5]. While most farming communities are sedentary and live in rural or urban areas, rainforest hunter-gatherers traditionally live in huts in the rainforest, moving regularly from one camp to another.

African rainforest hunter-gatherers (RHG)—collectively known by the historical and derogatory term ‘Pygmies’—are broadly subdivided into two groups that reflect their geographic location [6]. Western RHG inhabit the Congo Basin and include multiple populations such as the Baka, Aka, Koya or Bongo, whereas Eastern RHG live close to the Ituri rainforest and Lake Victoria and comprise groups such as the Asua, Sua, Efe or BaTwa. In addition to a forest-dwelling mode of subsistence, Western and Eastern RHG share distinctive cultural and phenotypic traits, such as specific hunting and honey-gathering techniques and a trait known as the ‘pygmy phenotype’, that is, small adult body size distinctive of certain African, Southeast Asian and South American populations [7]. African RHG, particularly those of the Ituri rainforest, show the lowest average adult stature worldwide, of <155 cm [8].

Bantu-speaking, agriculturalist populations of central Africa are thought to descend from early farming communities that recently expanded across sub-Saharan Africa [9]. The central African belt is also key in this respect, as it is adjacent to the postulated homeland of Bantu languages, where agriculture possibly emerged 3–5 Ky ago, in the area that corresponds today to Southeast Nigeria and Western Cameroon [3]. The appearance of pottery and polished stone tools within this time frame, together with the shared languages and oral traditions of farmers and hunter-gatherers, indicates an early and extensive history of economic and technological

exchanges between the ancestors of these two communities [1–3,8,10]. These contacts have been maintained until today; for example, some groups of rainforest hunter-gatherers remain sedentary for some time due to strong socioeconomic dependence on neighbouring farmers.

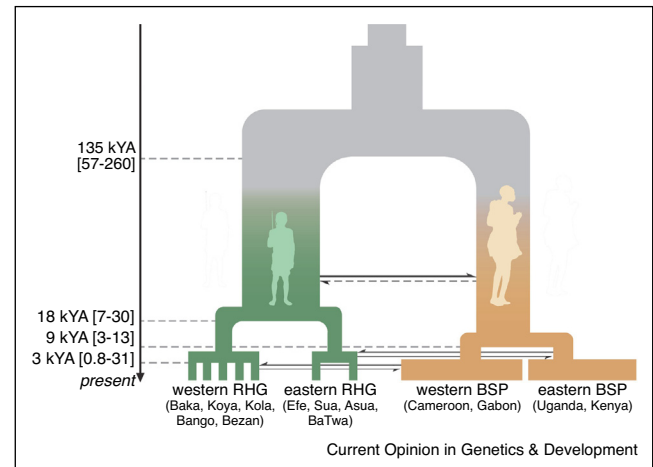
The lacks of archaeological data for central Africa, in particular for the Congo Basin owing to the rapid disintegration of fossil remains in the rainforest's acidic soils, have hampered the understanding of demography and adaptation of populations inhabiting this region. How the increasing availability of genomic data from populations of the region has counteracted this limitation is the goal of this review. We focus on how genomic studies of rainforest hunter-gatherers and farmers have been of paramount importance to infer their past demography — population splits, sizes changes and gene flow — as well as their history of biological adaptation, highlighting the importance of admixture as a possible source of new adaptive variation.

Deep divergence of central African populations in the Late Pleistocene

While the Late Pleistocene is thought to have witnessed modern human diversification within Africa [11], the human fossil record of central Africa is exceptionally sparse for this period [12]. The oldest samples studied have been dated at 20–25 Ky, and suggest that the biological and cultural diversity of central Africa during this period was considerable [13]. However, it is currently unknown if such diversity was a local exception, or a general rule in the diverse ecological regions composing central Africa.

The study of the genetic diversity of present-day populations represents an alternative, powerful approach to infer past population histories and ecologies. Population genetic studies have shown that present-day RHG and farming populations are characterized by one of the deepest splits in human evolution [14*,15*]. The combined modelling of 16 high-coverage whole genomes supports a separation of the ancestors of RHG and the west African Yoruba 90 Ky (85–92) or 155 Ky (139–164) ago, assuming either instantaneous or continuous asymmetric gene flow between the two groups [14*]. A similar approach recently applied on 300 exomes of RHG and Bantu-speaking farmers has estimated that their ancestors diverged 135 Ky (57–259) ago [15*] (Figure 1), assuming the most recent estimations of mutation rate [16] and generation time [17]. Under the same assumptions, the former study supports a population split as old as 300 Ky ago, while previous studies based on independent autosomal regions support a separation ~110 Ky ago [18,19]. Despite discrepancies between estimates, which may be due to imperfections in the models, low sample sizes, or the effects of background selection, they all support

Figure 1



A general demographic model of rainforest hunter-gatherer and farmer populations. This model recapitulates estimations of the demographic history of rainforest hunter-gatherers (RHG) and neighbouring Bantu-speaking farmer populations (BSP) of central Africa [15*,41,43]. Times are given in thousands of years from present (kYA). Inferred changes in effective population size are shown by changes in branch width, and gene flow by arrows.

ancient structure among the ancestors of rainforest hunter-gatherer and farmer populations, in agreement with the proposed human diversification within Africa during the Late Pleistocene [11].

Seminal ancient genomic studies have revealed that Neanderthals contributed ~2% of the genetic variation of present-day non-Africans [20–22], while Denisovans contributed ~5% of genetic variation to modern Melanesians [23–25]. Despite the coexistence throughout Africa of diverse forms of *Homo* with both archaic and modern traits during the Pleistocene [26], few studies have yet provided robust evidence of archaic introgression in Africa. Reference-free methods have nonetheless identified in RHG genomes hundreds of candidate introgressive loci, which are strongly depleted in genic regions [27–29]. Whether these observations reflect archaic admixture or ancestral structure [30] remains to be determined.

Demographic transitions and admixture during the Holocene

The Holocene in central Africa was characterized by a global warming after the Last Glacial Maximum, and the increase of forested areas followed by short episodes of forest contraction from 4 Ky onward [31,32]. These deforestation events were concomitant with the well-documented expansion of Bantu languages from the modern-day Nigeria-Cameroon border [3,33,34]. The Bantu expansion is thought as one of the most influential cultural events of African prehistory, as it spread a new, more

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