

Review



Cite this article: Boyette AH, Lew-Levy S, Jang H, Kandza V. 2022 Social ties in the Congo Basin: insights into tropical forest adaptation from BaYaka and their neighbours. *Phil. Trans. R. Soc. B* **377**: 20200490. <https://doi.org/10.1098/rstb.2020.0490>

Received: 11 July 2021
Accepted: 5 January 2022

One contribution of 15 to a theme issue
'Tropical forests in the deep human past'.

Subject Areas:
behaviour, ecology, ecosystems, evolution

Keywords:
hunter–gatherers, mobility, inter-group relations, Congo Basin, cultural adaptation

Author for correspondence:
Adam H. Boyette
e-mail: adam_boyette@eva.mpg.de

Social ties in the Congo Basin: insights into tropical forest adaptation from BaYaka and their neighbours

Adam H. Boyette¹, Sheina Lew-Levy^{1,2}, Haneul Jang¹ and Vidrige Kandza¹

¹Department of Human Behavior, Ecology and Culture and ²Department of Comparative Cultural Psychology, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, 04103 Leipzig, Germany

AHB, 0000-0003-0306-6841; SL-L, 0000-0002-1250-6418; HJ, 0000-0001-5994-6413

Investigating past and present human adaptation to the Congo Basin tropical forest can shed light on how climate and ecosystem variability have shaped human evolution. Here, we first review and synthesize genetic, palaeoclimatological, linguistic and historical data on the peopling of the Congo Basin. While forest fragmentation led to the increased genetic and geographical divergence of forest foragers, these groups maintained long-distance connectivity. The eventual expansion of Bantu speakers into the Congo Basin provided new opportunities for forging inter-group links, as evidenced by linguistic shifts and historical accounts. Building from our ethnographic work in the northern Republic of the Congo, we show how these inter-group links between forest forager communities as well as trade relationships with neighbouring farmers facilitate adaptation to ecoregions through knowledge exchange. While researchers tend to emphasize forager–farmer interactions that began in the Iron Age, we argue that foragers' cultivation of relational wealth with groups across the region played a major role in the initial occupation of the Congo Basin and, consequently, in cultural evolution among the ancestors of contemporary peoples.

This article is part of the theme issue 'Tropical forests in the deep human past'.

1. Introduction

Human evolution is classically portrayed as a story of adaptation to an emerging African savannah ecosystem. However, climatic and ecosystem variability is increasingly seen as the driving force in human evolution [1,2]. In this light, what adaptation to tropical forests can reveal about human evolution is relatively understudied. To address this gap, we first synthesize the archaeological, genetic and linguistic evidence for the expansion of humans into the Congo Basin and describe historical accounts of forager–farmer relations. Building from this evolutionary and historical perspective, we then describe the current social ties maintained by contemporary BaYaka foragers living along the Motaba river of the northern Republic of Congo. Throughout, we argue that the cultivation of relational wealth—that is, broadly, social ties that enable resource exchange and mutual assistance [3,4]—is central to forager adaptation. Particularly, links across forest forager communities in the Congo Basin, as well as trade relationships with neighbouring farmers and others (e.g. tradesmen, colonial administrators), support and have supported Congo Basin foragers' dynamic subsistence practices over time in the face of shifting political, economic and ecological landscapes.

2. Becoming forest specialists: migration into the Congo Basin

Genetic work paired with palaeoclimatic reconstruction suggests that the last common ancestor of contemporary Congo Basin foragers¹ and Bantu speakers

is estimated to have lived approximately 70 000 ya in present-day Cameroon and Gabon [13–15]. Maternal gene flow dating to 40 000 years ago (ya) suggests these ancestral groups likely maintained ties as the foragers' ancestors migrated into the forest [14]. The earliest presence of modern *Homo sapiens* in the Congo Basin is estimated to be at least 40 000 ya [16,17]. Sites throughout the Congo Basin suggest continued occupation of the region since before the Last Glacial Maximum (LGM), around 20 000 ya [17,18]. The Lupemban stone tool industry is found in sites that, based on faunal remains, palynology and palaeoclimatological evidence, reflect humans living in a mosaic of tropical forests, woodlands and savannahs across the region [17,19,20]. The presence of the Lupemban industry in different ecologies suggests technological continuity from the savannahs into the tropical forests throughout the late Pleistocene into the early Holocene [20].

After moving east into what is today the interior of the tropical forest, the two major genetic branches of the contemporary Congo Basin forager population diverged around 20–30 000 ya, forming the Western (e.g. Aka, Mbendjele, Baka and Bakola) and Eastern (Mbuti, Efe and Twa) genetic sub-groups [14,15,21,22]. It is likely that these two populations diverged during relatively dry, cooler periods during which the forest was highly fragmented [23,24]. Despite growing geographical and genetic distance, connections between Eastern and Western groups likely persisted. For example, divergence times for Y-chromosome haplotypes between the Western and Eastern groups date to between 10 000 and 15 000 ya, long after the LGM (19–26 500 ya [25], cited in [13]). These findings suggest continued male-mediated gene flow, consistent with general patterns of greater male mating and exploration ranges among contemporary Congo Basin foragers [26,27]. The Western group later further divided around 3000 ya [15].

Congo Basin tropical rainforests likely posed unique ecological challenges to the ancestors of contemporary foragers [28–30]. The region is a complex mosaic of micro-ecosystems varying in soil composition and patterns of inundation, resulting in diverse and seasonal concentrations of edible plants and animals [31]. Forest foods can lack micro-nutrients essential to the human diet, such as iodine [32], and the forests are also host to many parasitic infectious diseases [33]. Evidence suggests there was positive selection on relevant biological functions and pathways among Congo Basin foragers that would have facilitated adaptation to these challenges, including those involved in immunology, thyroid hormone pathways (i.e. possibly in response to iodine deficiency [32,34]), thermoregulation, lipid metabolism and growth and development [35–39].

Bantu speakers likely migrated to the forest periphery from the savannahs of Northwestern Cameroon between 3500 and 5000 ya [40–42]. Historical linguistic analysis suggests that these migrants were savannah-dwelling foragers [43]. Bantu-speaking Iron Age farmers then replaced or displaced these Neolithic savannah dwellers some 2500 ya [40–42]. Linguistic analyses suggest that contact between Bantu speakers and Congo Basin foragers likely had a major impact on the cultures and economies of the latter groups. In particular, languages spoken by foragers prior to contact were mostly abandoned in favour of the Bantu languages spoken by these migrants, with only some ancestral forest-oriented vocabulary remaining today [44]. These

cultural exchanges were dynamic, however, as indicated by the subsequent independent evolution of these languages within forager groups, and the fact that no foraging group today speaks the same language as the farming groups with whom they interact [12,45,46].

3. Maintaining inter-ethnic relationships: historical and ethnographic perspectives

Today, approximately 900 000 foragers live across nine countries in Central Africa [10], representing at least 15 ethnic groups [47,48] speaking 17 languages from six families [12,45]. Additionally, dozens of other ethnic groups, mostly Bantu-speaking farmers [49], subsist from shifting cultivation, fishing, commerce and a range of other practices [12,50,51].² Throughout the Congo Basin, forager–farmer relations are multi-dimensional and highly variable [12]. While founded upon economic exchange, authors differently emphasize exploitation by farmers [58], forager–farmer solidarity in the face of outside forces [52,55,59] or forager agency as 'hunters' of farmer resources [47,60]. These varying accounts nonetheless share the view that foragers maintain specialized and flexible subsistence knowledge and practices that have enabled both forager and farmer lifestyles throughout the region.

Pointing to the fact that sources of calories consumable by humans are scarce in rainforest settings, some have questioned whether foragers could subsist in the Congo Basin without access to cultigens from farmers [28–30,61]. Yet, contemporary foragers can and do live exclusively in the forest for extended periods of time [62–66]. Historical ecological data suggest that foragers themselves contribute to the propagation of wild yams [63,65]. Parts of *Dioscorea* tubers discarded during cooking lead to their dispersal, often in camps where light conditions from tree clearing favour growth [62]. Wild yams are also para-cultivated by reburying tuber parts with the intention of promoting their regeneration [65]. These practices highlight how forager activities and knowledge have likely shaped the availability and distribution of resources in the Congo Basin, which in turn can support forager communities [67].

Foragers are characterized by neighbouring farmers as the first inhabitants of the region [8,45–47,58]. Migrants, including Bantu speakers, historically depended on forager abilities and specialist knowledge to learn about their new forest environment [8,31,47,53]. Klieman [8] especially argues based on historical linguistic evidence that the foragers were essential to early farmer incursions into the forests, with different forager groups adopting roles as specialist procurers of forest products in exchange for iron, cultigens, and other material resources.

Farmer reliance on forager knowledge extended into the colonial period, when they served as default intermediaries between foragers and the states and corporations wishing to extract ivory, rubber, lumber and other commodities from the forest [9,46,53]. During this time, forager expertise and labour were critical to farmer political and economic survival, as the farmers, who were sedentary and held land, were subject to taxation by colonial powers. In exchange, foragers gained economic resources, including not only cultigens but knowledge of their cultivation, and social connections to tradesmen and colonial administrators with whom they

occasionally exchanged directly [9,44,51,68]. As such, foragers adapted their subsistence technologies to maximize their access to these resources. For instance, net hunting was adopted by foragers in the 1920s from Bantu-speaking farmers in response to colonial demands for duiker (*Cephalophus*) skins. The practice continued to be used opportunistically by some groups for decades, long after the market for pelts in France dried up [53,56,69,70].

4. Social links, diverse opportunities: a view from contemporary forest foragers

The nature of contemporary forager–farmer relations in the Congo Basin continues to be influenced by outside commercial, humanitarian and conservation interests in diverse ways [59,71–73]. Here, we describe how BaYaka foragers seek and integrate relational wealth into diverse livelihoods. We focus primarily on our work among several communities along the Motaba river in the Dongou District of the Likouala Department in the northern Republic of the Congo (figure 1). Along the Motaba, foragers identify as BaYaka/Aka³ [12,74–76]. From the upper Motaba downstream to the mouth of the river at Dongou, the largest farmer communities are Kaka, Bandongo and Bomitaba. Additionally, there are at least two villages inhabited by Ubangian speakers in the middle Motaba [12].

Along the Motaba, forager–farmer relationships are typically formalized within a fictive kinship framework. BaYaka are preferentially employed by farmer kin and perform their roles as family members during important events like births or deaths. Outside of the kinship framework, there are several BaYaka specialists hired by farmers to perform valued tasks. These include *nganga* traditional healers, who are sought for treatment or to identify the cause of an illness, and emcees who organize major gatherings such as funerals.

Via walking paths, the river and a growing system of roads, villages along the Motaba are linked socially and economically to each other, the rest of the region, the country and neighbouring parts of Central Africa. Below, we illustrate how mobility is woven into BaYaka social structure and culture, and how diverse, inter-group links contribute to their subsistence success.

(a) Growing up mobile

Mobility is central to BaYaka lifestyles. Individual and family ranges depend on the availability of food resources and opportunities for social interaction. In turn, mobility structures how and from whom BaYaka learn as they grow.

As immediate-return mobile hunter–gatherers with limited food storage, BaYaka houses tend to be small and close together [77]. Most social and economic activities are performed outside. People tend to maintain close physical proximity with others throughout the day [77–79]. In this setting, young children are given ample opportunities to participate in economic activities and build social relationships beyond their own nuclear family. Infants are often turned outward by those holding them to direct the child's attention to the surrounding people and activities [80]. As children grow, adults may ask them to perform increasingly complex tasks (e.g. from fetching items across camp to carrying messages kilometres away) as a means of engaging them

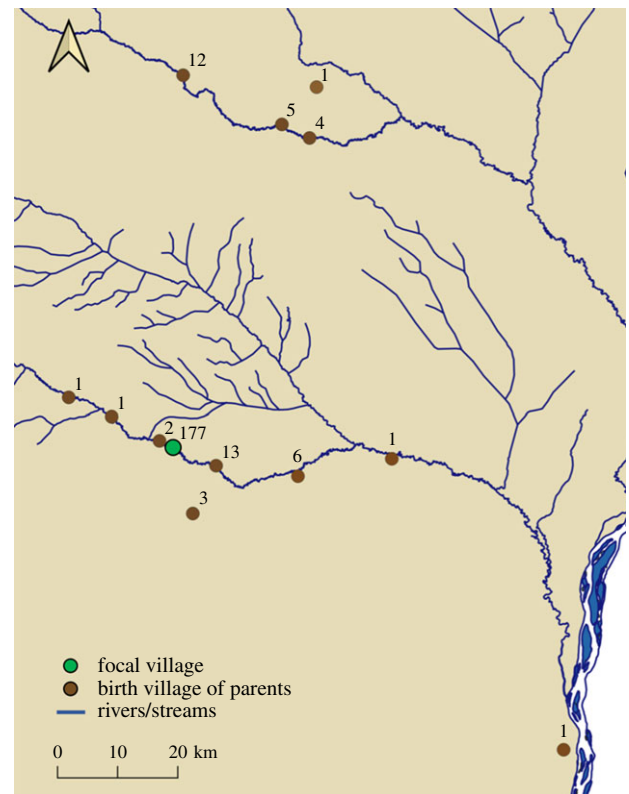


Figure 1. Regional connections to a Motaba village. In 2018, a sample of 124 individuals from the focal village along the Motaba (indicated by a green dot) reported the birth locations of their parents (brown dots). The numbers at each dot indicate the number of times the village was given as a birth location. This map shows inter-generational stability in the focal village but also reflects a snapshot of long-distance connectivity between communities in the region.

in daily routines ([81], also see [82]). A valued role for fathers in BaYaka culture is having children accompany them to the forest to learn during hunting and gathering trips [83,84]. With peers, children collaboratively learn subsistence knowledge and social norms essential to life in the forest and in society [85–88]. Most subsistence knowledge and skills are acquired before adolescence [89,90].

Residential groups are fluid, and the location of dwellings shifts in the context of seasonal mobility (figure 2). Many BaYaka along the Motaba spend approximately six months of the year in a multi-ethnic village setting. Villages are typically spatially segregated, with BaYaka and farmers residing in different neighbourhoods. BaYaka neighbourhoods can further be subdivided into hamlets that are loosely oriented around a core group of close kin (e.g. parents and their adult children, their affines and children). BaYaka regularly conduct day and overnight trips into the forest while settled in the village. In most villages, there are also two major periods of extended forest habitation: *kongo*, or caterpillar season from July to September, and *kombi*, or fish-weir season from October to December. In the forest, residential groupings are smaller and more dispersed with variable camp sizes. These camps are typically constituted by one or more families who also share a hamlet. The density of BaYaka houses seen in figure 2 reflects the social density of life in smaller forest camps.

The inset in figure 2 shows the geographical distribution of one family's seasonal camps. Of note is a forest garden 9.86 km from the village (in straight line distance). Most

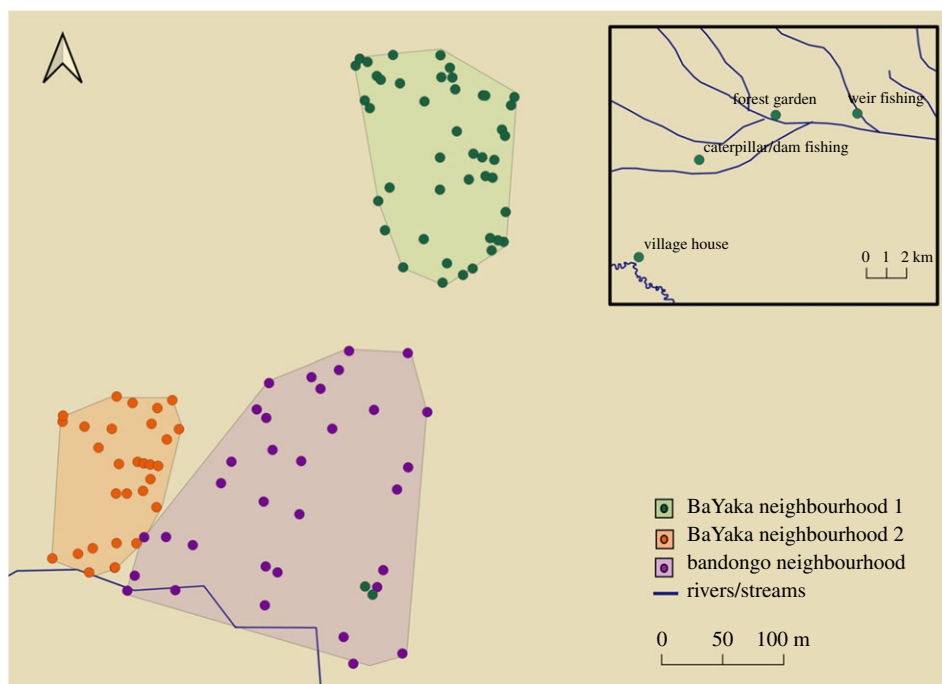


Figure 2. A multi-ethnic, spatially segregated village. This village has three neighbourhoods, two BaYaka and one Bandongo. Each point is a house marked from 2015 to 2018. Note that a BaYaka family from the northern community lived with a Bandongo family on their compound at the time for a period of labour exchange. *Inset:* One BaYaka household's seasonal residences and the location of their agricultural plot in the forest.

BaYaka have forest gardens, knowledge of which they say their ancestors acquired from farmers. Importantly, these gardens require little direct input. As gardens mature, they are more often used as 'storehouses', with crops left to grow and reproduce on their own [91], a practice continuous with the process of encouraging wild *Dioscorea* yams to grow by clearing spaces in the forest [62,67]. The BaYaka family who planted the aforementioned forest garden did so with the specific intent of gaining independence from their farmer neighbours. Having this forest garden allows them to spend months away from the village while still maintaining access to cultigens.

Mobility is especially pronounced in adolescence and young adulthood, when finding a spouse from outside the local community is a priority [26]. The locations marked on figure 1 indicate the reported birth locations of the parents of 124 people living in one village (green dots) along the Motaba (data collected in 2018). The largest distance between where a parent was born and their adult child now lives is 82.4 km. As residence is multilocal [70,92], inter-community marriages give individuals and their families opportunities to build relational wealth. Indeed, traits that promote building the relational wealth of the community (e.g. sharing, welcoming) are seen as valued aspects of fatherhood among the BaYaka [83]. Mobility is central to the flow of knowledge throughout the Congo Basin, including of subsistence innovations [93–95], medicinal plants [88] and forest spirit dances [96].

Throughout history, Congo Basin foragers have used mobility as a strategy to avoid exploitative trade relationships, with individuals or groups moving deeper into the forest or searching for new farmer trade partners [46,97,98]. As the region has become more market-integrated, farmers continue to maintain trade relationships with the BaYaka, whose forest products are sold to urban centres in exchange for market goods or cash. The increasing pressure to school BaYaka children further impedes BaYaka mobility, with

school calendars often conflicting with foraging activities [98]. Choosing to remain close to market towns has also been linked to decreases in traditional plant knowledge and preferences for traditional medicine [99], increases in wealth inequalities and a greater future-oriented time preference [100]. Still, while schooling may limit BaYaka mobility as it relates to forest activities, it may also place BaYaka in contact with new ideas and people [101]. Roads may increase BaYaka mobility, especially as it relates to labour opportunities. BaYaka in market towns continue to participate in the economy of forest spirits, with some reportedly investing up to four months' worth of wages into new dances [96]. These findings hint at the fact that while patterns may change, mobility will likely continue to be foundational to BaYaka identity and cultural practices.

(b) Subsistence flexibility in a heterogenous ecosystem

There is considerable ecological variability along the Motaba river. Some villages are situated in Congolian Lowland Forests where streams do not typically go dry. Others are situated in a Western Congolian Swamp Forest ecoregion. These villages are located at higher elevation, have drier forest and are only seasonally inundated. Reflecting local subsistence adaptations to these ecoregions, villages along the Motaba practice differing fishing strategies [102].

Weir (*kombi*) and dam (*doka*) fishing are widely practiced fishing techniques along the Motaba. Unique to swamp forest ecoregions is *mosongo* fishing. *Mosongo* fishing uses permanent, human-dug fishponds and is practiced after *kombi* season has finished. Thus, for those with access rights to the ponds, *mosongo* can extend fishing seasons in the forest.

Mosongo has only recently been reported along the Motaba [102]. The geographically closest prior reports of *mosongo* are from several groups of Bantu C-20 language-speakers in the southern part of the ecoregion in the Cuvette some 300 km away [103]. There, inland fishing is a major

economic activity, and pond fishing is widely practiced. It is possible that *mosongo* along the Motaba originated from traditional Bantu fishing in the southern floodplains and was spread to Likouala Bantu groups. This possibility is supported by the observation that Bantu-speaking people from Motaba villages, Impfondo, and Brazzaville travel to swamp forests to participate in pond fishing [102]. Typically, Bantu have access rights to multiple ponds inherited from their mothers or grandmothers.

While BaYaka labour at the Bantu ponds in exchange for a portion of fish, they also have their own ponds inherited through the maternal line [102]. These are typically located further into the forest. The fish collected for the visiting Bantu fisher–farmers are sold commercially, while in their own ponds, the BaYaka collect fish for their subsistence, or for sale at regional markets. Cash earned is primarily used to restock on flashlights, batteries and other commercial goods that they use throughout the year. *Mosongo* fishing demonstrates how inter-group relationships expose BaYaka to novel subsistence practices, and the ease with which BaYaka incorporate these into their cultural repertoire.

(c) Hunting and global intersections

Consistent with historical accounts cited above, farmers along the Motaba claim their ancestors learned about the local ecology through the economic and social relations forged with BaYaka. BaYaka exchange products with farmers daily, including palm wine, *Irvingia excels* and *Treculia africana* nuts, and honey. They are also employed in making palm oil and corn liquor and as labour in gardens and for house construction. In exchange, farmers provide iron, salt, clothes and other agricultural and market products. Game meat is one of the most important forest products the BaYaka acquire for trade with their farmer neighbours [104].

As a result of taboos and the BaYaka's minimal access to cash, farmers are typically the exclusive owners of shotguns. As forest specialists, BaYaka are frequently tasked with hunting with these guns. Farmers will then sell bushmeat, earning a significant cash profit of 1000% or more per bullet. BaYaka hunters are typically paid with the 'hunter's portion' of head, tail and entrails. BaYaka hunters make the best of this situation by keeping some animals while reporting to farmers that they 'missed shots' [104]. Thus, BaYaka use their forest knowledge and skill as well as the Bantu dependence on these traits to their own advantage.

Due to conservation policies and logging, shotgun hunting may make BaYaka increasingly vulnerable [105]. Hunting endangered species is illegal, posing a major risk for hunters who can serve jail time for poaching. Road construction and the increased demand for bushmeat driven by logging are associated with increased sedentism and alcoholism among BaYaka hunters [53,71,106,107]. Because of logging activities, smaller and smaller sections of the forest are available for subsistence activities [108,109]. The likelihood of environmental degradation and game population decline has the potential to tip the balance from cooperation to exploitation of BaYaka shotgun hunters. At the same time, as game becomes increasingly rare and/or dispersed, shotguns may become one of the last viable technologies through which to successfully hunt [110]. In this context, the current rapid anthropogenic loss of the forest tests the strength of BaYaka mobility and relational wealth to buffer environmental changes.

5. Discussion

Biological adaptations to the pathogen-rich and relatively nutrient-poor ecology of the Congo Basin have undoubtedly been foundational to the continuous occupation of the region by forest foragers. In this paper, we have argued that alongside these biological adaptations, the cultivation of widespread inter-group relationships helped foragers develop subsistence practices adapted to the complex, closed canopy, humid tropical rainforest. We have further suggested that farmer expansion into the Congo Basin was dependent on forager knowledge of the forest. While we have focused here on the Congo Basin, social connections between distant and diverse groups are likely foundational to human adaptation more generally [4,111–116]. The movement of people, their genes, their things and their ideas across a wide expanse of Africa and beyond has shaped our species' evolutionary history [111,117,118].

Research has converged on a model of forager social structure in which groups have relatively low relatedness between their members as a result of the density of affinal kin [119,120]. Between groups, ties are maintained through marriage and close friendships [88,115]. These ties theoretically and empirically increase the efficiency of information flow [88,114,115]. The multiple, dynamic and large-scale linguistic shifts we have reviewed here further suggest that forest foragers have maintained a flexible and opportunistic strategy in relations with other groups, including with Bantu migrants, as part of a general strategy of building relational wealth and ensuring access to a broad range of resources and information across the challenging tropical forest landscape [8,46,53].

Despite extensive archaeological, historic and ethnographic evidence that diverse forager groups have formed a breadth of relationships with farmers, pastoralists and other non-foragers (e.g. for reviews: [121–123]), the adaptive role of these inter-group relationships has received relatively little attention [8,47]. Yet inter-group cooperation helps communities to withstand resource shortfalls and provides access to non-locally available resources [124–126]. Especially within biodiverse regions such as the Congo Basin tropical forest, niche specialization facilitates adaptation through trading informational (e.g. ecological knowledge, techniques), material (e.g. tools, forest foods, cultigens, imported market goods), cultural (e.g. meanings, beliefs, practices) and social (e.g. marriages, specialists, friendships) resources [127]. Such inter-group cooperation may help explain the observed linguistic diversity in highly biodiverse lower latitude ecologies in Africa and globally [128].

Foragers have always lived in shifting cultural and ecological landscapes. Whereas forest contraction and expansion drove forager mobility and inter-group exchange in the Congo Basin's past, the intertwined forces of market integration, schooling, logging, climate change and conservation efforts by outsiders are principal drivers today. Their effects on forager livelihoods vary considerably [73,106,129]. Continued research into Congo Basin forager patterns of mobility and interconnectedness in response to such forces has the potential to yield further insights into the micro-scale processes that led to human adaptation to tropical forests.

Ethics. Ethics for 2018 data collection were obtained from the University of Cambridge (PRE.2018 0.023).

Data accessibility. The data used in this paper include GPS coordinates for locations of villages and people's houses to illustrate general spatial patterns. For reasons of privacy, we cannot make these data public. Requests for specific use of these data for research purposes can be made by contacting the corresponding author and will be judged on a case-by-case basis.

Authors' contributions. A.H.B.: conceptualization, data curation, writing—original draft, writing—review and editing; S.L.-L.: conceptualization, data curation, writing—review and editing; H.J.: data curation, visualization, writing—review and editing; V.K.: data curation, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Competing interests. We declare we have no competing interests.

Funding. We received no funding for this study.

Acknowledgements. The authors thank DZABATOU Ardain for help in preparing figure 1, MEKOUNOU Paul for contributions in gathering data for figure 2 and Senay Cebioğlu for helpful comments on an earlier draft of this manuscript. We also thank all of the people along the Motaba and from Brazzaville who continue to help us understand adaptation to the tropical forests of the Congo Basin.

Endnotes

¹Throughout, we choose not to use the terms 'Pygmy' or 'Pygmies' but instead use forager/foragers when writing generally, or the

particular ethnonym of the group discussed as their name has been published (e.g., BaYaka, Baka). The term 'Pygmy' is in wide and continued use by academics across disciplines (e.g. [5–10]) as well as in the popular press. In the Congo Basin, the term is often used pejoratively by other ethnic groups to indicate 'backwardness' or being less than human, and can be used to admonish others for unacceptable behaviour *within* Congo Basin forager societies as well. However, it has also been reappropriated by many foragers for self-reference and connotes to them their unique identity vis-à-vis 'non-Pygmies' [11,12]. Our choice reflects how we would communicate about identity among our interlocutors in the Congo Basin.

²We use the terms 'foragers' and 'farmers' or 'fisher-farmers' to contrast the two major groups found throughout the Congo Basin, each of which is constituted by peoples of multiple ethnicities. We recognize that these terms gloss over significant diversity in subsistence practices maintained by peoples in the region and that there is important overlap across the groups. Moreover, peoples' identities are shaped by more than how they acquire their food, such that these terms are not holistic labels [52]. Again, we use local ethnonyms whenever possible, but for purposes of generalization, we follow a tradition of work using these terms to compare these groups [7,47,53–57] and believe that at a minimum they connote the major ecological and economic relations of these societies that their core cultural features reflect and support.

³These people have been referred to by both terms. We use 'BaYaka' after Lewis [11] as it is inclusive of the different forest forager groups differentiated by the foragers themselves, including Ngabo, Ngombe and Mbendjele.

References

- Kaboth-Bahr S *et al.* 2021 Paleo-ENSO influence on African environments and early modern humans. *Proc. Natl Acad. Sci. USA* **118**, e2018277118. (doi:10.1073/pnas.2018277118)
- Potts R, Faith JT. 2015 Alternating high and low climate variability: the context of natural selection and speciation in Plio-Pleistocene hominin evolution. *J. Hum. Evol.* **87**, 5–20. (doi:10.1016/j.jhevol.2015.06.014)
- Borgerhoff Mulder M *et al.* 2009 Intergenerational wealth transmission and the dynamics of inequality in small-scale societies. *Science* **326**, 682–688. (doi:10.1126/science.1178336)
- Bird DW, Bird RB, Codding BF, Zeanah DW. 2019 Variability in the organization and size of hunter-gatherer groups: foragers do not live in small-scale societies. *J. Hum. Evol.* **131**, 96–108. (doi:10.1016/j.jhevol.2019.03.005)
- Bahuchet S. 1985 *Les Pygmées Aka et la forêt Centrafricaine*. Paris, France: SELAF.
- Chaudhary N, Salali GD, Thompson J, Dyble M, Page A, Smith D, Mace R, Migliano AB. 2015 Polygyny without wealth: popularity in gift games predicts polygyny in BaYaka pygmies. *R. Soc. Open Sci.* **2**, 150054. (doi:10.1098/rsos.150054)
- Hewlett BS *et al.* 2014 *Hunter-gatherers of the Congo basin: cultures, histories and biology of African pygmies*. New Brunswick, NJ: Transaction Publishers.
- Klieman KA. 2003 *The pygmies were our compass: Bantu and Batwa in the history of west Central Africa, early times to c. 1900 C.E.* Portsmouth, NH: Heinemann.
- Lewis J. 2005 Whose forest is it anyway? Mbendjele Yaka pygmies, the Ndoki forest and the wider world. In *Property and equality volume 2: encapsulation, commercialisation, discrimination* (eds T Widlock, WG Tadesse), pp. 56–78. New York, NY: Berghahn Books.
- Olivero J *et al.* 2016 Distribution and numbers of pygmies in central African forests. *PLoS ONE* **11**, e0144499. (doi:10.1371/journal.pone.0144499)
- Lewis J. 2002 Forest hunter-gatherers and their world: a study of the Mbendjele Yaka Pygmies of Congo-Brazzaville and their secular and religious activities and representations. Doctoral thesis, London School of Economics and Political Science, London, UK.
- Takeuchi K. 2014 Interethnic relationships between pygmies and farmers. In *Hunter-gatherers of the Congo Basin: cultures, histories, and biology of African pygmies* (ed. BS Hewlett), pp. 299–320. New Brunswick, NJ: Transaction Publishers.
- Batini C *et al.* 2011 Signatures of the preagricultural peopling processes in sub-Saharan Africa as revealed by the phylogeography of early Y chromosome lineages. *Mol. Biol. Evol.* **28**, 2603–2613. (doi:10.1093/molbev/msr089)
- Quintana-Murci L *et al.* 2008 Maternal traces of deep common ancestry and asymmetric gene flow between pygmy hunter-gatherers and Bantu-speaking farmers. *Proc. Natl Acad. Sci. USA* **105**, 1596–1601. (doi:10.1073/pnas.0711467105)
- Verdu P *et al.* 2009 Origins and genetic diversity of pygmy hunter-gatherers from Western Central Africa. *Curr. Biol.* **19**, 312–318. (doi:10.1016/j.cub.2008.12.049)
- Mercader J, Martí R, González IJ, Sánchez A, García P. 2003 Archaeological site formation in rain forests: insights from the Ituri Rock Shelters, Congo. *J. Archaeol. Sci.* **30**, 45–65. (doi:10.1006/jasc.2002.0810)
- Mercader J, Brooks AS. 2001 Across forests and savannas: later stone age assemblages from Ituri and Semliki, Democratic Republic of Congo. *J. Anthropol. Res.* **57**, 197–217. (doi:10.1086/jar.57.2.3631567)
- Mercader J, Martí R. 2001 The Middle Stone Age occupations of Atlantic Central Africa: new evidence from Equatorial Guinea and Cameroon. In *Under the canopy: the archaeology of tropical rainforests* (ed. J Mercader), pp. 64–92. Piscataway, NJ: Rutgers University Press.
- Cornelissen E. 2002 Human responses to changing environments in Central Africa between 40 000 and 12 000 B.P. *P. J. World Prehistory* **16**, 197–235. (doi:10.1023/A:1020949501304)
- Taylor N. 2011 The origins of hunting and gathering in the Congo Basin: a perspective on the Middle Stone Age Lupemban industry. *Farming* **1**, 1–20.
- Batini C *et al.* 2011 Insights into the demographic history of African pygmies from complete mitochondrial genomes. *Mol. Biol. Evol.* **28**, 1099–1110. (doi:10.1093/molbev/msq294)
- Patin E, Quintana-Murci L. 2018 The demographic and adaptive history of central African hunter-gatherers and farmers. *Curr. Opin. Genet. Dev.* **53**, 90–97. (doi:10.1016/j.gde.2018.07.008)
- Hamilton AC, Taylor D. 1992 History of climate and forests in tropical Africa during the last 8 million years. In *Tropical forests and climate* (ed. N Myers), pp. 65–78. Dordrecht, Netherlands: Springer.
- Miller CS, Gosling WD, Kemp DB, Coe AL, Gilmour I. 2016 Drivers of ecosystem and climate change in tropical West Africa over the past ~540 000 years. *J. Quat. Sci.* **31**, 671–677. (doi:10.1002/jqs.2893)

25. Clark PU, Dyke AS, Shakun JD, Carlson AE, Clark J, Wohlfarth B, Mitrovica JX, Hostetler SW, McCabe AM. 2009 The last glacial maximum. *Science* **325**, 710–714. (doi:10.1126/science.1172873)
26. MacDonald DH, Hewlett BS. 1999 Reproductive interests and forager mobility. *Curr. Anthropol.* **40**, 501–523. (doi:10.1086/200047)
27. Cavalli-Sforza LL, Hewlett B. 1982 Exploration and mating range in African pygmies. *Ann. Hum. Genet.* **46**, 257–270. (doi:10.1111/j.1469-1809.1982.tb00717.x)
28. Bailey RC, Headland TN. 1991 The tropical rain forest: is it a productive environment for human foragers? *Hum. Ecol.* **19**, 261–285. (doi:10.1007/BF00888748)
29. Hart TB, Hart JA. 1986 The ecological basis of hunter-gatherer subsistence in African rain forests: the Mbuti of eastern Zaire. *Hum. Ecol.* **14**, 29–55. (doi:10.1007/BF00889209)
30. Bailey RC, Head G, Jenike M, Owen B, Rechtman R, Zechenter E. 1989 Hunting and gathering in tropical forest: is it possible? *Am. Anthropol.* **91**, 59–82. (doi:10.1525/aa.1989.91.1.02a00040)
31. Bahuchet S. 1988 Food supply uncertainty among the Aka pygmies (Lobaye, Central African Republic). In *Coping with uncertainty in food supply* (eds I de Garine, GA Harrison). Oxford, UK: Oxford University Press.
32. Dormitzer PR, Ellison PT, Bode HH. 1989 Anomalously low endemic goiter prevalence among Efe pygmies. *Am. J. Phys. Anthropol.* **78**, 527–531. (doi:10.1002/ajpa.1330780408)
33. Guernier V, Hochberg ME, Guégan J-F. 2004 Ecology drives the worldwide distribution of human diseases. *PLoS Biol.* **2**, e141. (doi:10.1371/journal.pbio.0020141)
34. López Herráez D *et al.* 2009 Genetic variation and recent positive selection in worldwide human populations: evidence from nearly 1 million SNPs. *PLoS ONE* **4**, e7888. (doi:10.1371/journal.pone.0007888)
35. Perry GH, Verdu P. 2017 Genomic perspectives on the history and evolutionary ecology of tropical rainforest occupation by humans. *Quat. Int.* **448**, 150–157. (doi:10.1016/j.quaint.2016.04.038)
36. Amorim CEG, Daub JT, Salzano FM, Foll M, Excoffier L. 2015 Detection of convergent genome-wide signals of adaptation to tropical forests in humans. *PLoS ONE* **10**, e0121557. (doi:10.1371/journal.pone.0121557)
37. Migliano AB *et al.* 2013 Evolution of the pygmy phenotype: evidence of positive selection from genome-wide scans in African, Asian, and Melanesian pygmies. *Hum. Biol.* **85**, 251–284. (doi:10.3378/027.085.0313)
38. Tishkoff SA *et al.* 2009 The genetic structure and history of Africans and African Americans. *Science* **324**, 1035–1044. (doi:10.1126/science.1172257)
39. Lopez M *et al.* 2019 Genomic evidence for local adaptation of hunter-gatherers to the African rainforest. *Curr. Biol.* **29**, 2926–2935. (doi:10.1016/j.cub.2019.07.013)
40. Grollemund R, Branford S, Bostoen K, Meade A, Venditti C, Pagel M. 2015 Bantu expansion shows that habitat alters the route and pace of human dispersals. *Proc. Natl Acad. Sci. USA* **112**, 13 296–13 301. (doi:10.1073/pnas.1503793112)
41. Bostoen K, Clist B, Doumenge C, Grollemund R, Hombert J-M, Muluwa JK, Maley J. 2015 Middle to late Holocene paleoclimatic change and the early Bantu expansion in the rain forests of Western Central Africa. *Curr. Anthropol.* **56**, 354–384. (doi:10.1086/681436)
42. Oslisly R, White L, Bentaieb I, Favier C, Fontugne M, Gillet J-F, Sebago D. 2013 Climatic and cultural changes in the west Congo Basin forests over the past 5000 years. *Phil. Trans. R. Soc. B* **368**, 20120304. (doi:10.1098/rstb.2012.0304)
43. Bostoen K, Muluwa JK. 2017 Were the first Bantu speakers south of the rainforest farmers?: A first assessment of the linguistic evidence. In *Language dispersal beyond farming* (eds M Robbeets, A Saveliev), pp. 235–258. Amsterdam, The Netherlands: John Benjamins Publishing Company.
44. Bahuchet S. 1993 History of the inhabitants of the central african rain forest: perspectives from comparative linguistics. In *Tropical forests, people and food: biocultural interactions and applications to development* (eds CM Hladik, A Hladik, OF Linares, H Pagezy, A Semple, M Hadley), pp. 37–55. Paris, France: UNESCO and The Parthenon Publishing Group.
45. Bahuchet S. 2012 Changing language, remaining pygmy. *Hum. Biol.* **84**, 11–43. (doi:10.3378/027.084.0101)
46. Moise RE. 2014 'Do pygmies have a history?' revisited: The autochthonous tradition in the history of Equatorial Africa. In *Hunter-gatherers of the Congo basin: cultures, histories, and biology of African pygmies* (ed. BS Hewlett), pp. 85–116. New Brunswick, NJ: Transaction Publishers.
47. Köhler A, Lewis J. 2001 Putting hunter-gatherer and farmer relations in perspective: a commentary from Central Africa. In *Ethnicity, hunter-gatherers, and the 'other': association or assimilation in Africa* (ed. S Kent), pp. 276–306. Washington, DC: Smithsonian Institution Press.
48. Verdu P, Destro-Bisol G. 2012 African pygmies, what's behind a name? *Hum. Biol.* **84**, 1–10. (doi:10.3378/027.084.0105)
49. Güldemann T, Winkhart B. Forthcoming. The *Baakaa and other puzzles: foraging and farming peoples in the western Central African Rainforest. *Anthropol. Linguist.*
50. Komatsu K. 1998 The food cultures of the shifting cultivators in Central Africa: the diversity in selection of food materials. *Afr. Study Monogr. Suppl.* **25**, 149–177.
51. Terashima H. 1986 Economic exchange and the symbiotic relationship between the Mbuti (Efe) pygmies and the neighbouring farmers. *Sprache Gesch. Afr.* **7**, 391–406.
52. Rupp S. 2011 *Forests of belonging: identities, ethnicities, and stereotypes in the Congo river basin*. Seattle, WA: University of Washington Press.
53. Bahuchet S, Guillaume H. 1982 Aka-farmer relations in the northwest Congo Basin. In *Politics and history in band societies* (eds EB Leacock, RB Lee), pp. 189–212. Cambridge, UK: Cambridge University Press.
54. Fouts HN. 2004 Social and emotional contexts of weaning among Bofi farmers and foragers. *Ethnology* **43**, 65–81. (doi:10.2307/3773856)
55. Grinker RR. 1990 Images of denigration: structuring inequality between foragers and farmers in the Ituri Forest, Zaire. *Am. Ethnol.* **17**, 111–130. (doi:10.1525/ae.1990.17.1.02a00070)
56. Hewlett BS. 1991 *Intimate fathers: the nature and context of Aka pygmy paternal infant care*. Ann Arbor, MI: University of Michigan Press.
57. Meehan CL, Roulette JW. 2013 Early supplementary feeding among central African foragers and farmers: a biocultural approach. *Soc. Sci. Med.* **96**, 112–120. (doi:10.1016/j.socscimed.2013.07.029)
58. Vansina J. 1990 *Paths in the rainforests: towards a history of political tradition in equatorial Africa*. Madison, WI: The University of Wisconsin.
59. Joiris DV. 2003 The framework of Central African hunter-gatherers and neighbouring societies. *Afr. Study Monogr. Suppl.* **28**, 57–79.
60. Turnbull CM. 1962 *The forest people*. New York, NY: Simon & Schuster.
61. Headland TN. 1987 The wild yam question: how well could independent hunter-gatherers live in a tropical rain forest ecosystem? *Hum. Ecol.* **14**, 463–491. (doi:10.1007/BF00888000)
62. Yasuoka H. 2013 Dense wild yam patches established by hunter-gatherer camps: beyond the wild yam question, toward the historical ecology of rainforests. *Hum. Ecol.* **41**, 465–475. (doi:10.1007/s10745-013-9574-z)
63. Yasuoka H. 2006 Long-term foraging expeditions (Molongo) among the Baka hunter-gatherers in the northwestern Congo Basin, with special reference to the 'wild yam question'. *Hum. Ecol.* **34**, 275–296. (doi:10.1007/s10745-006-9017-1)
64. Hladik CM, Dounias E. 1993 Wild yams of the African forest as potential food resources. In *Tropical forests, people, and food: biocultural interactions and applications to development* (eds CM Hladik, A Hladik, OF Linares, A Semple, M Hadley), pp. 163–176. Paris, France: UNESCO.
65. Dounias E. 2001 The management of wild yam tubers by the Baka pygmies in southern Cameroon. *Afr. Study Monogr. Suppl.* **26**, 135–156.
66. Sato H. 2001 The potential of edible wild yams and yam-like plants as a staple food resource in the African tropical rain forest. *Afr. Study Monogr. Suppl.* **26**, 123–134.
67. Ichikawa M. 2012 Central African forests as hunter-gatherers' living environment: an approach to historical ecology. *Afr. Study Monogr. Suppl.* **43**, 3–14.
68. Wilkie DS, Curran B. 1993 Historical trends in forager and farmer exchange in the Ituri rain forest of Northeastern Zaire. *Hum. Ecol.* **21**, 389–417. (doi:10.1007/BF00891141)

69. Noss AJ. 1997 The economic importance of communal net hunting among the BaAka of the Central African Republic. *Hum. Ecol.* **25**, 71–89. (doi:10.1023/A:1021935903440)
70. Kitanishi K. 1998 Food sharing among the Aka hunter-gatherers in Northeastern Congo. *Afr. Study Monogr.* **25**, 3–32.
71. Riddell M. 2013 Assessing the impacts of conservation and commercial forestry on livelihoods in Northern Republic of Congo. *Conserv. Soc.* **11**, 199. (doi:10.4103/0972-4923.121002)
72. Kenrick J, Lewis J. 2001 Discrimination against the forest people ('pygmies') of Central Africa. In *Racism against indigenous peoples*. Copenhagen, Denmark: IWGIA Document.
73. Kidd C, Kenrick J, Couillard V, Gilbert J. 2009 *Land rights and the forest peoples of Africa: historical, legal and anthropological perspectives*. Moreton-in-March, UK: Forest Peoples Programme.
74. Bombjaková D. 2018 The role of public speaking, ridicule, and play in cultural transmission among Mbendjele BaYaka forest hunter-gatherers. Doctoral Dissertation, University College London, London, UK.
75. Kano T, Asato R. 1994 Hunting pressure on chimpanzee and gorillas in the Motaba River Area, Northeastern Congo. *Afr. Study Monogr.* **15**, 143–162. (doi:10.14989/68121)
76. Kitanishi K. 1994 The exchange of forest products (*Irvingia* nuts) between the Aka hunter-gatherers and the cultivators in Northeastern Congo. *Tropics* **4**, 79–92. (doi:10.3759/tropics.4.79)
77. Hewlett BS, Hudson J, Boyette AH, Fouts HN. 2019 Intimate living: Sharing space among Aka and other hunter-gatherers. In *Towards a broader view of hunter-gatherer sharing* (eds D Friesem, N Lavi), pp. 39–56. Cambridge, UK: McDonald Institute for Archaeological Research.
78. Boyette AH. Accepted. Cultural niche construction supports low-cost, high-fidelity learning of techniques: the example of blade tool use among BaYaka forager children in the Republic of the Congo. In *Flexibility and rigidity in the use and transmission of techniques* (eds M Charbonneau, D Sperber).
79. Lewis J. 2014 Egalitarian social organization: The case of the Mbendjele BaYaka. In *Hunter-gatherers of the Congo basin: cultures, histories, and biology of African pygmies* (ed. BS Hewlett), pp. 219–244. New Brunswick, NJ: Transaction Publishers.
80. Hewlett BS, Roulette CJ. 2016 Teaching in hunter-gatherer infancy. *R. Soc. Open Sci.* **3**, 150403. (doi:10.1098/rsos.150403)
81. Boyette AH, Lew-Levy S. 2021 Socialization, autonomy, and cooperation: insights from task assignment among the egalitarian BaYaka. *Ethos* **48**, 12284. (doi:10.1111/etho.12284)
82. Lew-Levy S, Crittenden AN, Boyette AH, Mabulla IA, Hewlett BS, Lamb ME. 2019 Inter- and intra-cultural variation in learning-through-participation among Hadza and BaYaka forager children and adolescents from Tanzania and the Republic of the Congo. *J. Psychol. Afr.* **29**, 309–318. (doi:10.1080/14330237.2019.1647957)
83. Boyette AH, Lew-Levy S, Sarma MS, Valchy M, Gettler LT. 2020 Fatherhood, egalitarianism, and child health in two small-scale societies in the Republic of the Congo. *Am. J. Hum. Biol.* **32**, e23342. (doi:10.1002/ajhb.23342)
84. Lew-Levy S, Milks A, Kiabiya Ntamboudila F, Broesch T, Kline MA. 2021 BaYaka adolescent boys nominate accessible adult men as preferred spear hunting models. *Curr. Anthropol.* **62**, 631–640.
85. Lew-Levy S, Kissler SM, Boyette AH, Crittenden AN, Mabulla IA, Hewlett BS. 2020 Who teaches children to forage? Exploring the primacy of child-to-child teaching among Hadza and BaYaka hunter-gatherers of Tanzania and Congo. *Evol. Hum. Behav.* **41**, 12–22. (doi:10.1016/j.evolhumbehav.2019.07.003)
86. Lew-Levy S, Reckin R, Lavi N, Cristóbal-Azkarate J, Ellis-Davies K. 2017 How do hunter-gatherer children learn subsistence skills?: a meta-ethnographic review. *Hum. Nat.* **28**, 367–394. (doi:10.1007/s12110-017-9302-2)
87. Lew-Levy S, Lavi N, Reckin R, Cristóbal-Azkarate J, Ellis-Davies K. 2018 How do hunter-gatherer children learn social and gender norms? *Meta-Ethnogr. Rev. Cross-Cult. Res.* **52**, 213–255. (doi:10.1177/1069397117723552)
88. Salali GD *et al.* 2016 Knowledge-sharing networks in hunter-gatherers and the evolution of cumulative culture. *Curr. Biol.* **26**, 2516–2521. (doi:10.1016/j.cub.2016.07.015)
89. Hewlett BS, Cavalli-Sforza LL. 1986 Cultural transmission among Aka pygmies. *Am. Anthropol.* **88**, 922–934. (doi:10.1525/aa.1986.88.4.02a00100)
90. Lew-Levy S, Ringen EJ, Crittenden AN, Mabulla IA, Broesch T, Kline MA. 2021 The life history of learning subsistence skills among Hadza and BaYaka foragers from Tanzania and the Republic of Congo. *Hum. Nat.* **32**, 16–47. (doi:10.1007/s12110-021-09386-9)
91. Kramer KL, Greaves RD. 2016 Diversify or replace: what happens to wild foods when cultigens are introduced into hunter-gatherer diets? In *Why forage? Hunters and gatherers in the twenty-first century*, pp. 15–42. Santa Fe, NM: School for Advanced Research Press.
92. Matsuura N. 2015 Human female dispersal and social organization: a case of central African hunter-gatherers. In *Dispersing primate females* (eds T Furuichi, J Yamagiwa, F Aureli), pp. 165–183. Tokyo, Japan: Springer.
93. Hewlett BL. 2013 'Ekeloko': The spirit to create-Innovation and social learning among Aka adolescents of the Central African Rainforest. In *Dynamics of learning in neanderthals and modern humans*, vol. 1 (eds T Akazawa, Y Nishiaki, K Aoki), pp. 187–195. Tokyo, Japan: Springer.
94. Hewlett BL. 2016 Innovation, processes of social learning, and modes of cultural transmission among the Chabu adolescent forager-farmers of Ethiopia. In *Social learning and innovation in contemporary hunter-gatherers* (eds H Terashima, BS Hewlett), pp. 203–215. Tokyo, Japan: Springer.
95. Hewlett B. 2021 Social learning and innovation in adolescence: a comparative study of Aka and Chabu hunter-gatherers of Central and Eastern Africa. *Hum. Nat.* **32**, 239–278. (doi:10.1007/s12110-021-09391-y)
96. Lewis J. 2015 Where goods are free but knowledge costs: hunter-gatherer ritual economics in Western Central Africa. *Hunt. Gatherer Res.* **1**, 1–27. (doi:10.3828/hgr.2015.2)
97. Lewis J. 2005 Whose forest is it anyway? Mbendjele Yaka pygmies, the Ndoki forest and the wider world. In *Property and equality*, vol. 2: *encapsulation, commercialisation, discrimination* (eds T Widlock, WG Tadesse), pp. 1–6. New York, NY: Berghahn Books.
98. Bombjaková D, Lew-Levy S, Duda R, Loubelo B, Lewis J. Under review BaYaka education: from the forest to the ORA (Observer, Réflexir, Agir) classroom. *Hunt. Gatherer Res.*
99. Salali GD *et al.* 2020 Global WEIRDing: transitions in wild plant knowledge and treatment preferences in Congo hunter-gatherers. *Evol. Hum. Sci.* **2**, e24. (doi:10.1017/ehs.2020.26)
100. Salali GD, Migliano AB. 2015 Future discounting in Congo basin hunter-gatherers declines with socio-economic transitions. *PLoS ONE* **10**, e0137806. (doi:10.1371/journal.pone.0137806)
101. Ninkova V, Hays J, Lavi N, Ali A, Lopes da Silva Macedo S, Davis HE, Lew-Levy S. 2022. Hunter-gatherer children at school: a view from the global south. *PsyArXiv*. (doi:10.31234/osf.io/zxq98)
102. Jang H, Boyette AH. 2021. Observations of cooperative pond fishing by the Bayaka and Bantu People in the flooded forest of the Northern Republic of Congo. *Afr. Study Monogr.* **41**, 1–16. (doi:10.34548/asm.41.2.1)
103. Comptour M, Caillon S, McKay D. 2016 Pond fishing in the Congolese cuvette: a story of fishermen, animals, and water spirits. *Rev. D'ethnoécologie* **10**, 1–27. (doi:10.4000/ethnoecologie.2795)
104. Kandza V, Jang H, Lew-Levy S, Boyette AH. Forthcoming. The dynamics of inter-ethnic cooperation in for-hire shotgun hunting among BaYaka and Yambe of the Republic of the Congo.
105. Duda R, Gallois S, Reyes-García V. 2017 Hunting techniques, wildlife offtake and market integration. A perspective from individual variations among the Baka (Cameroon). *Afr. Study Monogr.* **38**, 97–118. (doi:10.14989/225259)
106. Oishi T, Hayashi K. 2014. From ritual dance to disco: Change in habitual use of tobacco and alcohol among the Baka hunter-gatherers of southeastern Cameroon. *Afr. Study Monogr.* **47**, 143–163. (doi:10.14989/185097)
107. Knight JK, Salali GD, Sikka G, Derx I, Keestra SM, Chaudhary N. 2021 Quantifying patterns of alcohol consumption and its effects on health and wellbeing among BaYaka hunter-gatherers: a mixed-methods cross-sectional study. *PLoS ONE* **16**, e0258384. (doi:10.1371/journal.pone.0258384)
108. Wilkie DS, Sidle JG, Boundzanga GC. 1992 Mechanized logging, market hunting, and a bank loan in Congo. *Conserv. Biol.* **6**, 570–580. (doi:10.1046/j.1523-1739.1992.06040570.x)

109. Wilkie DS, Carpenter JF. 1999 Bushmeat hunting in the Congo Basin: an assessment of impacts and options for mitigation. *Biodivers. Conserv.* **8**, 927–955. (doi:10.1023/A:1008877309871)
110. Hames RB. 1979 A comparison of the efficiencies of the shotgun and the bow in neotropical forest hunting. *Hum. Ecol.* **7**, 219–252.
111. Scerri EML *et al.* 2018 Did our species evolve in subdivided populations across Africa, and why does it matter? *Trends Ecol. Evol.* **33**, 582–594. (doi:10.1016/j.tree.2018.05.005)
112. Whallon R. 2006 Social networks and information: non-'utilitarian' mobility among hunter-gatherers. *J. Anthropol. Archaeol.* **25**, 259–270. (doi:10.1016/j.jaa.2005.11.004)
113. Romano V, Lozano S, Fernández-López de Pablo J. 2020 A multilevel analytical framework for studying cultural evolution in prehistoric hunter-gatherer societies. *Biol. Rev.* **95**, 1020–1035. (doi:10.1111/brv.12599)
114. Hill KR, Wood BM, Baggio J, Hurtado AM, Boyd RT. 2014 Hunter-gatherer inter-band interaction rates: implications for cumulative culture. *PLoS ONE* **9**, e102806. (doi:10.1371/journal.pone.0102806)
115. Migliano AB *et al.* 2017 Characterization of hunter-gatherer networks and implications for cumulative culture. *Nat. Hum. Behav.* **1**, 0043. (doi:10.1038/s41562-016-0043)
116. Boyd R, Richerson PJ. 2021 Large-scale cooperation in small-scale foraging societies. (doi:10.32942/osf.io/fxwbr)
117. McBrearty S, Brooks AS. 2000 The revolution that wasn't: a new interpretation of the origin of modern human behavior. *J. Hum. Evol.* **39**, 453–563. (doi:10.1006/jhev.2000.0435)
118. Bergström A, Stringer C, Hajdinjak M, Scerri EML, Skoglund P. 2021 Origins of modern human ancestry. *Nature* **590**, 229–237. (doi:10.1038/s41586-021-03244-5)
119. Hill KR *et al.* 2011 Co-Residence patterns in hunter-gatherer societies show unique human social structure. *Science* **331**, 1286–1289. (doi:10.1126/science.1199071)
120. Dyble M, Gardner A, Vinicius L, Migliano AB. 2018 Inclusive fitness for in-laws. *Biol. Lett.* **14**, 20180515. (doi:10.1098/rsbl.2018.0515)
121. Myers FR. 1988 Critical trends in the study of hunter-gatherers. *Annu. Rev. Anthropol.* **17**, 261–282. (doi:10.1146/annurev.an.17.100188.001401)
122. Spielmann KA, Eder JF. 1994 Hunters and farmers: then and now. *Annu. Rev. Anthropol.* **23**, 303–323. (doi:10.1146/annurev.an.23.100194.001511)
123. Wilmsen EN, Denbow JR. 1990 Paradigmatic history of San-speaking peoples and current attempts at revision. *Curr. Anthropol.* **31**, 489–524. (doi:10.1086/203890)
124. Pisor AC, Surbeck M. 2019 The evolution of intergroup tolerance in nonhuman primates and humans. *Evol. Anthr. Issues News Rev.* **28**, 210–223. (doi:10.1002/evan.21793)
125. Robinson EJM, Barker JL. 2017 Inter-group cooperation in humans and other animals. *Biol. Lett.* **13**, 20160793. (doi:10.1098/rsbl.2016.0793)
126. Pisor AC, Gurven M. 2016 Risk buffering and resource access shape valuation of out-group strangers. *Sci. Rep.* **6**, 30435. (doi:10.1038/srep30435)
127. Smith EA. 2001 On the coevolution of cultural, linguistic, and biological diversity. In *On biocultural diversity: linking language, knowledge, and the environment* (ed. L Maffi), pp. 95–117. Washington, DC: Smithsonian Institution Press.
128. Moore JL, Manne L, Brooks T, Burgess ND, Davies R, Rahbek C, Williams P, Balmford A. 2002 The distribution of cultural and biological diversity in Africa. *Proc. R. Soc. B* **269**, 1645–1653. (doi:10.1098/rspb.2002.2075)
129. Ichikawa M. 2014 Forest conservation and indigenous peoples in the Congo Basin: New trends toward reconciliation between global issues and local interest. In *Hunter-gatherers of the Congo basin: cultures, histories, and biology of African pygmies* (ed. BS Hewlett), pp. 321–342. New Brunswick, NJ: Transaction Publishers.